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THE BOTANICAL REVIEW

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THE VEGETATION OF ALBERTA

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INTRODUCTION

Scope of Review

The Province of Alberta, Canada, holds more than ordinary interest for botanists, especially for specialists in phytogeography, taxonomy and ecology. This is mainly because it is a region of vegetational transition zones. Here, two great plant formations, steppe and forest, come together, having east-west and north-south ecotones, as well as outliers, one within the other. Here also, is the meeting ground of east (Atlantic) and west (Pacific) floras or, more precisely, of boreal and Cordilleran elements. Moreover, in the north of the Province, transition from boreal to arctic begins.

Vast areas of the region are still unknown botanically, and many of the published reports are to be regarded as preliminary and tentative. Nevertheless, the literature is now of sufficient coverage and extent to warrant a review and general appraisal. Moreover, a synthesis of present knowledge would seem to serve a useful purpose in focussing attention on some of the main issues and unsolved problems. Not all aspects of our subject can be covered, of course, even within the compass of a fairly long review. Nor is it

necessary in this review to deal with certain topics, notably, problems of boreal-arctic vegetation and floristics. These and related topics have already been discussed in excellent articles by Raup (1941, 1946, 1947b). Certain other features of our plant life are arbitrarily excluded from consideration in this review, viz., algae, fungi, introduced plants and cultivated crops of all kinds. Publications dealing with taxonomic revisions of plants of our region also receive no attention, though references are made to available manuals, catalogues and species lists. The main emphasis is on synecological aspects of our vegetation, with particular reference to the prairie and forest associations of southern and central Alberta, the northern portion of the Province having been dealt with in recent comprehensive papers. The presentation is generally in terms of communities, succession and monoclimax; however, for certain mountain forests, the " continuum " concept and the climax as a " variable pattern " find favor. It is hoped that the review may interest those who are concerned with these concepts. Our discussion of prairie parkland includes a few excerpts from writings of early explorers. These and various later publications serve to show how our present understanding of the vegetation has been reached.

Description of the Region

Only a general account of the physical features, soils and climate will be presented. Reference may be made to publications by Allan, Wyatt et al., Odynsky et al., Raup, Lewis et al., as well as to earlier papers by the present writer, for more detailed information.

PHYSICAL FEATURES. According to Allan (1943), Alberta has an area of approximately 255,285 square miles, and extends from the 49th parallel to lat. 60° north, a distance of 756 miles. The width of the Province averages about 325 miles. The west boundary is the Continental Divide in the Rocky Mountains north to about lat. 54°; it then follows longitude 120° to lat. 60°.

In Alberta there are four major physical divisions, namely, mountains, foothills, plains, and, lastly, the Precambrian area which is in the extreme northeastern corner of the Province and has an area of about 8000 square miles (Allan, 1943). The plains division comprises 87 per cent of the total area of the region. The lowest part of Alberta is in the northeastern corner, where the

altitude is about 650 feet above sea level. The plains division, often described as an undulating plateau, varies in elevation from 800 to 1000 in the north to about 3,500 feet along the eastern edge of the foothills belt. There are several prominences rising a few hundreds of feet above the surrounding plain, the highest including the Caribou Mountains in the north, the Swan Hills south of Lesser Slave Lake, and the Cypress Hills in southeastern Alberta. Sharp relief is provided by several great river valleys which run east and north. Lakes are very numerous in certain regions. In the south these are for the most part shallow basins (" sloughs ") which become partially dried up during the hot summer season. Northward the forested region is dotted with lakes, varying in size from a few hundred feet across to great bodies of water like Lesser Slave Lake, 50 miles long, and Lake Athabasca, 160 miles long. Many of the smaller lakes in the north are surrounded by peat bog. There is no sharp line of demarcation between the plains and the foothills belt. The foothills exhibit a rolling topography with elevations ranging generally from 3,000 to 5,000 feet above sea level. The mountain division (the Rocky Mountains) has elevations ranging from 3,500 feet along some of the valleys up to about 12,000 feet in the highest mountains.

GEOLOGY AND SOILS. The exposed strata in Alberta include rocks varying in age from the Precambrian to the early Tertiary age. In the mountains the oldest rocks are exposed, made up chiefly of limestones, sandstones, quartzites and shales. The soils within the mountains have been formed locally from these rocks (Allan, 1943). A recent report (Crossley, 1951) on the soils at Kananaskis, west of Calgary, appears to be the first detailed forest soil survey done in the Canadian Rocky Mountains and is an important contribution to knowledge of mountain soils and their relationships. A considerable proportion of the soils in the area of the survey are podsolic (brown and grey). In the foothills, Allan describes the rocks as folded and broken, consisting chiefly of sandstones, shales and coal seams. Most of the soils in the valleys and lowlands between the foothill ridges have been derived from the decayed rock on the ridges, and partly from outwash from the mountains. The plains are underlain, in large part, by rock formations chiefly younger and softer than those in the foothills belt.

Much of Alberta is covered by glacial deposits of Pleistocene age. Ice sheets from two sources extended over a large part of the plains and foothills of Alberta. The Keewatin ice sheet reached our region from the northeast and left debris chiefly from Precambrian rocks. Cordilleran glaciers flowed eastward as a piedmont ice sheet from the front of the mountains. This ice sheet left debris consisting largely of rock from the mountains where limestones and dolomites predominate (Allan, 1943). Large areas of Alberta are covered by resorted glacial deposits, and other large areas by alluvial and lacustrine materials transported by running water. Still other areas are occupied by residual material developed from the underlying rock formations.

From these various deposits, through the action of climatic and biotic factors, the soils of the region have developed. Major soil zones, named after prevailing color of surface horizons are Brown, Dark Brown, Black, Transition (Grey Black) and Grey Wooded (Fig. 1). Following Wyatt et al. (1938–43) and Odynsky (1945a), these soil zones may be characterized briefly as follows. Brown soils, found in the semi-arid southeastern area, have a brown profile with an A-horizon of about five inches and a lime layer some 15 inches below the surface. Dark-brown soils have an A-horizon of about seven inches and a lime layer 20 to 24 inches below the surface. Black soils, found in the parkland region, where rainfall is higher and evaporation lower, have a black or deep brown horizon of 10 to 14 inches and a lime accumulation at 24–40 inches. Transition (grey-black) soils occur mainly in woodland and show mixed profiles ranging from black to nearly grey. Grey-wooded soils characterize forested areas in much of northern and northwestern Alberta, and are relatively less fertile than the other types. They have developed under humid soil moisture conditions and have a surface horizon of semi-decomposed leaf mold, a severely leached and platy, greyish A-horizon of six to eight inches. Some of these grey-wooded soils are described as podsolic. Brief reference has already been made to soils of the Rocky Mountain region. Extensive peat areas also occur in central and northern Alberta.

CLIMATE. In general the climate of Alberta is representative of continental regions of northern latitudes, being characterized by a relatively low annual precipitation and by great extremes in tem-

perature between summer and winter seasons. However, striking differences in climatic conditions are found within the region. Southeastern Alberta has an average annual precipitation of about 12 inches, a high rate of evaporation, frequent hot dry winds and prolonged periods of drought. Northward and northwestward, the annual precipitation increases to about 18 inches in central Alberta and then decreases to 12 inches or less in northern areas. Over the same territory the evaporation rate decreases and hot winds are less frequent or rare. "In the more northern parts of Alberta the somewhat shorter growing season, the lower temperature, and the greater proportion of cloudiness compensate for the lower precipitation and make tree growth possible on most kinds of terrain" (Moss, 1952). Westward across southern Alberta the precipitation increases markedly to 20 or 25 inches in the foothills and to as much as 30 inches in the mountains. Sanderson (1948) classifies the foothills and mountains of Alberta as "moist subhumid", having little or no water deficiency in any season. All other portions of the Province are said by Sanderson to have little or no water surplus in any season and are classified as "dry subhumid" to "semiarid", the latter being the condition in the southeast.

FLORA—CATALOGUES, LISTS, MANUALS

The botanical classic "Flora Boreali-Americana" by W. J. Hooker (1829–40), based on collections of early explorers, contains the first comprehensive account of the plants of northern Alberta. Macoun's (1883–90) "Catalogue of Canadian Plants" includes records of his own extensive collections as well as earlier reports of species for Alberta as a whole. A few lists of limited scope were published in the early part of the present century, including that of Edith Farr (1907) on our mountain flora and one by Standley (1912) on the Mount Robson region.

Rydberg's (1917) Rocky Mountain Flora was the first manual assaying to cover Alberta, at least south of 55° N., and still is the only manual with that coverage of the Province. Rydberg's (1932) Plains Flora is quite useful for southeastern Alberta. A recent and very acceptable publication by Budd (1952), with descriptions of some 1200 vascular plants, covers the prairie and main parkland areas of the Province. Though a comprehensive manual for the

Alberta flora is still to appear, much of the necessary ground work has been done. Several lists and catalogues based on extensive field work have been published for representative areas. There has also been a certain amount of critical taxonomic work on some of the collections. First and foremost are the excellent annotated catalogues of Raup (1934, 1935, 1936, 1942) for portions of northern Alberta. Turner (1949) has provided a splendid list of the vascular plants of the south-central region, centering on Edmonton. For the Cypress Hills, in southeastern Alberta, Breitung's (1954) catalogue is an important contribution. Forthcoming catalogues covering some of our mountain areas are awaited with interest. Breitung has in manuscript an annotated list of the vascular plants of Waterton Lakes Park, and A. E. Porsild is preparing an illustrated manual on the Flora of the Rocky Mountain National Parks. Several of the ecological papers reviewed below contain lists of species and floristic notes. Reference should also be made to publications on the plants of areas adjoining Alberta. Of special significance are the critical studies of Porsild and Raup (1943) and Raup (1947a) on regions north of Alberta. The excellent Saskatchewan List by Fraser and Russell (1954) is consulted regularly by Alberta botanists, as also are the Flora of southern British Columbia (Henry, 1915) and the recent Supplement to this Flora (Eastham, 1947). A manual by Standley (1921) on the flora of Glacier National Park is quite useful for southwestern Alberta. Of interest, too, is the publication of a flora of Montana, the first part of which has appeared (Booth, 1950).

Reference may also be made to a number of semi-popular treatments of our flora and to certain briefer lists of species. Attractively illustrated books include the Alpine Flora by Brown and Schäffer (1907), the book on mountain wild flowers by Henshaw (1915), and the interesting account of wild flowers by McCalla (1920). A more recent book (Hardy and Hardy, 1949) on plants of the Rockies illustrates 200 wild flowers in color. A bulletin by Shoemaker (1938) on trees and shrubs in Alberta deals with native as well as exotic forms, especially in relation to their culture. Cormack (1948) lists the orchids of the Cypress Hills, with special mention of a few rare forms of *Orchis and Corallorhiza.* Groh (1949) has published notes on numerous native species, as well

as weeds, for Peace River and Fort Vermilion areas. Grasses of our region are described by Clarke et al. (1944), with particular reference to their identification by means of vegetative characters.

Though this review concerns itself mainly with vascular plants, special mention is made of bryophytes and lichens in connection with reports on certain types of vegetation. Species of these groups are listed in several of the papers reviewed. Reference may also be made to papers on lichens of the north by Lucy C. Raup (1928, 1930) and lichens of the mountain forest by Brinkman (1937); also to a list of Alberta liverworts by Brinkman (1923). Other papers on lichens and bryophytes by Brinkman are cited by Moss and McCalla (1946).

PHYTOGEOGRAPHIC PROBLEMS

(Relict Areas and Postglacial Forests)

Discussion of phytogeographic topics is largely excluded from the present review. However, a brief presentation of certain of these topics is required as a setting for a consideration of synecological data. Apart from the subject of phytogeographic regions or life zones (see below), there are intriguing floristic problems that demand at least passing mention.

As has often been pointed out, Alberta is a meeting ground of eastern and western floras. This is exemplified by pairs of closely related species (vicariants), such as *Pinus banksiana* and *P. contorta, Abies balsamea* and *A. lasiocarpa, Populus balsamifera* and *P. trichocarpa,* in eastern and western regions. These floras present interesting problems concerning the origin and history of our vegetation, especially in terms of Pleistocene events and more recent climatic fluctuations. Various outliers of Boreal and Cordilleran vegetation, one within the other, serve to complicate the picture. However, critical study of the outliers as possible relict areas of a former vegetation, may actually help to clarify our understanding of the past. Alberta provides a somewhat similar situation in its Steppe-Forest transition (discussed later in this review).

Possible Cordilleran relict areas are the tops of the Caribou Mountains, the Swan Hills and the Cypress Hills. There is some evidence that these areas escaped glaciation as nunataks, but whether any vegetation survived on these nunataks is problem-

atical. In a recent discussion of the Cypress Hills, Breitung (1954) says it is not improbable that the submontane forest and grassland actually persisted there during the last glaciation. He notes, however, that Russell (1951) favors the view that the Cordilleran biota reached the Cypress Hills in early post-glacial time, subsequent to the northeasterly retreat of the ice front. As the climate became warmer the Cordilleran element withdrew to the higher elevation of the Hills, to become segregated from the mountains by a broad belt of prairie.

Unglaciated areas in our foothills region may have served as refugia for biota during the period of the Wisconsin ice-sheets. Though the Cordilleran and Keewatin sheets coalesced at several points during times of greatest advance, it is unlikely that they united along the entire front. The pertinent geological evidence has been reviewed by Hansen (1949a, 1949b, 1950, 1952) in connection with his pollen analyses of peat sections in Alberta and British Columbia. Hansen (1950) reaches the general conclusions that " an ice-free corridor, 100 miles or more in width, existed between the Keewatin and Cordilleran ice sheet during the late Wisconsin glaciation " and that " the abundance of spruce and pine . . . as indicated in the lowest horizons of peat bogs in the region, suggests that this ice-free area was forested during Late Wisconsin or soon thereafter ". Forests of this foothills refugium are believed to have been centers from which biota migrated into progressively deglaciated areas. Alternate advances and recessions of the ice-sheets flanking the refugium may have occurred, bringing about corresponding shifts in the vegetation and possibly isolation of biota (as relicts) in certain locations.

Of further interest in this connection is the refugium believed to have existed during the Late Wisconsin in the upper Yukon River valley. " How extensive an ice-covered area separated the unglaciated portion of Yukon Territory and the ice-free corridor of western Alberta during the Late Wisconsin glacier is at present conjectural ". Whether pine and spruce, migrating northward from western Alberta or southward from the Yukon, were the first to reach the intervening region, is impossible to say (Hansen, 1950). Involved here is Hultén's (1937) theory of the persistence of plants in unglaciated refugia in the Yukon and Alaska, and especially his view that continental western American radiants

from a Beringia center had migrated southward before the Wisconsin glaciation and persisted in ice-free areas close to or within the icefront during at least the Late Wisconsin stage (Hansen, 1949b). With particular reference to peat profiles of bogs in west-central Alberta, Hansen suggests that they may record pre-Late-Wisconsin forests that had persisted in an ice-free corridor during this glacial stage, and so lend support to Hultén's view.

A review of Hultén's (1937) important contribution to phytogeography is beyond the purview of the present article, but the following references are to be noted. In the light of Hultén's theory, Halliday and Brown (1943) draw certain inferences with regard to the relationship of some forest tree species to present climate and the possible course followed in their repopulation of the Canadian land-mass following Wisconsin glaciation. Hultén's work has been discussed in comprehensive articles by Raup (1941, 1946, 1947a, 1947b). Of special significance would appear to be Raup's critical examination of the flora of the Mackenzie Mountains in the light of Hultén's thesis concerning the origin and dispersal of all arctic and boreal floras.

PHYTOGEOGRAPHIC REGIONS (Life Zones)

Several attempts have been made to define biogeographic areas, such as life zones, biotic provinces, vegetation belts and phytogeographic regions. The general result is one of considerable confusion in concepts and terminology. For our present purpose, a modified form of Halliday's (1937) classification has been adopted (Fig. 1 and Table I). To justify our concepts and terms, also to show the bearing on pertinent synecological categories, the following review is presented.

Merriam's well known life zones, though now largely discredited, are worthy of some attention here. Odum (1953) points out that a "major life zone", as understood by European ecologists, is not the same as "life zone" as used in North America. On this Continent "life zone" generally has reference to a series of temperature zones proposed by C. H. Merriam in 1894 and widely used by zoologists. According to Odum, the original temperature criteria have been abandoned, and Merriam's life zones are currently based on the distribution of organisms. Indeed, these zones have tended to become community zones, actu-

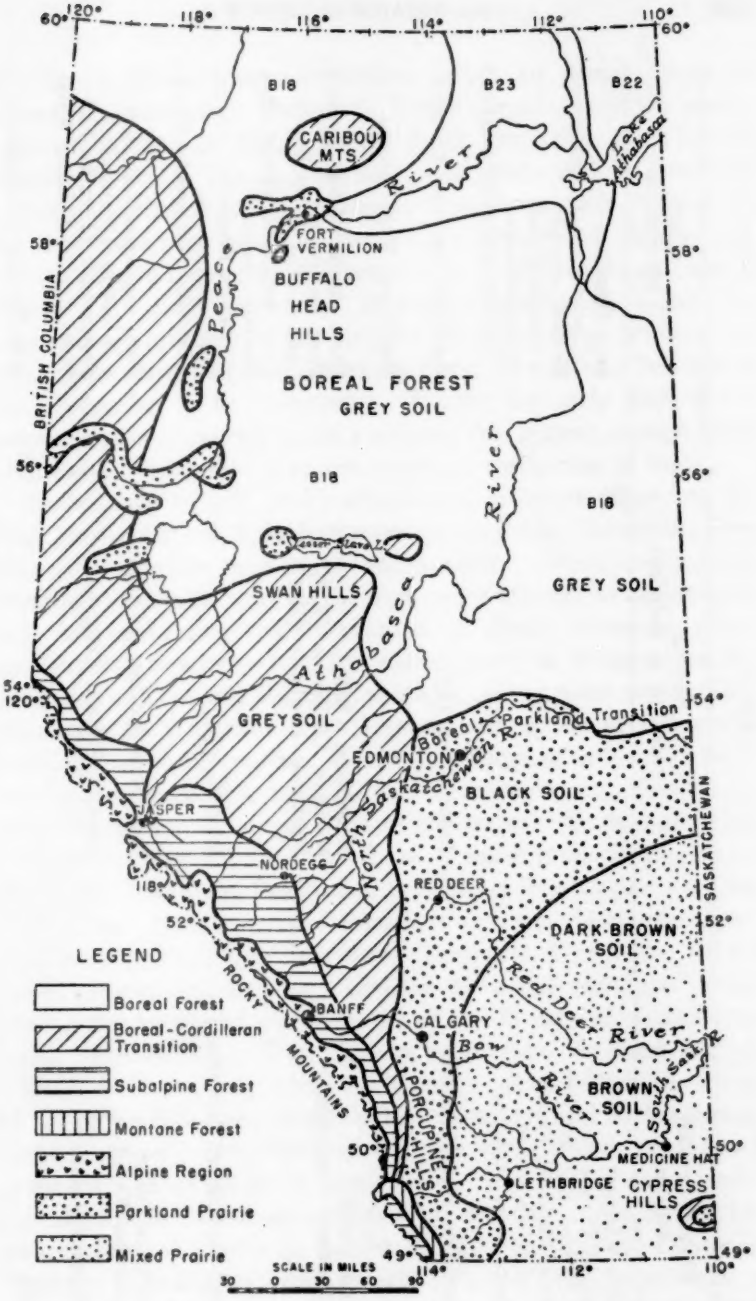

FIG. 1. Outline map of the Province of Alberta, showing the main phytogeographic regions.

TABLE 1

Phytogeographic regions	Sections (According to Halliday)	Chief communities
Prairie (Steppe) Mixed Prairie (Brown Soil Belt) Main Parkland Prairie (Black Soil Belt) Peace River Parkland		Stipa-Bouteloua (Spear grass–Grama grass) Festuca scabrella (Rough fescue) Agropyron-Stipa (Wheat grass–Spear grass)
Boreal-Grassland Transition	Aspen Grove (B17)	Populus tremuloides (Aspen)
		Marsh and Reed Swamp
Boreal Forest (Northern Coniferous)	Mixedwood (B18) Northern Coniferous (B22) Mackenzie Lowlands (B23)	Picea glauca (White Spruce) Picea mariana, Larix laricina } Bog Forest Pinus banksiana (Jack Pine) Populus (Aspen) (Balsam Poplar)
Boreal-Cordilleran Transition	Foothills (B19)	Pinus contorta var. latifolia (Lodgepole Pine)
Cordilleran Forest Subalpine Forest	East Slope Rockies (SA1)	Picea engelmanni–Abies lasiocarpa (Spruce-Fir)
Montane Forest	Douglas Fir and Lodgepole Pine (M5)	Pseudotsuga (Douglas Fir) Pinus flexilis (Limber Pine)
Alpine		Miscellaneous Communities

ally biome divisions or subdivisions in all but name. Most of Alberta is included in Merriam's Boreal Region, only the southwestern plains area falling in the Arid Transition Zone of his Austral Region. The Boreal Region is subdivided by Merriam (1898) into three zones: Arctic-alpine, represented in Alebrta by the treeless alpine areas of the Rocky Mountains; Hudsonian, which includes the northern forested part of our region and also a similar belt just below the timberline southward along the mountains; Canadian, which includes the forest lying between the Hudsonian Zone and the Transition Zone, as well as a belt below the Hudsonian in the mountains. During the early part of the present century, various authors adopted this system, though often with major changes in boundaries and in application of terms.

Daubenmire (1938, 1946) shows how different efforts to delimit Hudsonian and Canadian zones in the Rocky Mountains have proven inadequate and often inconsistent. While recognizing Merriam's life-zone work as the first major attempt to use climatic data in interpreting the distribution of North American biota, Daubenmire concludes that life zones based on temperature are untenable and are best delimited as major climax plant associations. Moreover, he maintains that Merriam's terms are arbitrary and meaningless; therefore, they should be abandoned in favor of more descriptive names that apply to precise concepts, e.g., Engelmann spruce–subalpine fir zone. Use of the terms "Hudsonian" and "Canadian" for subdivisions of the Transcontinental Region or Northern Coniferous Forest has proven no less fortunate. Dice (1943), for example, recognizes as Hudsonian a "biotic province" that includes the entire Northern Coniferous Forest east of the Rocky Mountains, and as Canadian a "biotic province" comprising the hardwood forest climax of the Great Lakes and eastward. According to Dice, approximately the northern half of Alberta is Hudsonian, while the Cordilleran and Plains portions of our region fall, respectively, in his Montanian and Saskatchewan biotic provinces. Broad divisions similar to the "biotic provinces" proposed by Dice are by no means new. For northern and western Canada, Dice's Eskimonian, Hudsonian, Montanian and Saskatchewan correspond closely to the Arctic, Transcontinental (Boreal), Western (Cordilleran) and Prairie (Plains) Regions of various authors, e.g., Adams and Senn (1945). The latter terms appear

to have the advantage of being fairly descriptive and generally understood.

Significant as these major biotic regions may be, more ecological interest probably attaches to their major subdivisions, especially those commonly recognized as biotic associations. Reference may be made here to the terms " montane " and " subalpine " for subdivisions of the Western (Cordilleran) Region. These have been variously employed by different authors, including Rydberg (1917), Halliday (1937) and Spilsbury and Tisdale (1944). According to Daubenmire's (1946) critical analysis, the Subalpine Zone is approximately the Hudsonian Zone as usually understood; it is also the *Picea-Abies* association of Weaver and Clements (1938) and the spruce-fir zone of Daubenmire (1942). The Montane Zone is included in the Canadian Zone of earlier authors and is the *Pinus-Pseudotsuga* association of Weaver and Clements; it is equivalent to the Douglas-fir zone of Daubenmire. Actually, the term " montane " has been variously applied, as have " Hudsonian " and " Canadian " already discussed. Daubenmire (1946) wishes to reject the term " subalpine " for any one unit because subalpine vegetation differs considerably from one mountain system to another. He suggests that the only terminology free from these criticisms is that based upon the dominant and characteristic species of a zone, e.g., " Engelmann spruce–subalpine fir " zone.

In the light of foregoing considerations, a vegetational classification is presented (Table I) which incorporates features of Halliday's (1937) forest system and which aims to relate familiar concepts and terminology of biogeographers, foresters and ecologists. Halliday's classification has the advantage of utilizing terms that are, in the main, descriptive of the vegetation types or of the terrain. His designations (B17 to M5) for different forest subdivisions are included in Table I for the benefit of Canadian foresters and others who use the system. Of the concepts and terms proposed, " Montane " is perhaps the least satisfactory for our purpose. As will be explained later, the so-called Montane Forest, as it occurs in Alberta, is recognized rather better by shrub and herb strata than by the characteristic tree dominants. Despite Daubenmire's objections to " Subalpine ", this term is retained as being generally understood and readily applied in our region. We

prefer to treat Halliday's Foothills Section (B19) as a Boreal-Cordilleran Transition rather than a Section of the Boreal. Any one particularly interested in the forests of northeastern Alberta should be aware of Raup's (1946) criticisms of Halliday's Sections B22 and B23. The main purpose of Table I is to set forth the relationship of the various phytogeographic regions and subdivisions to the chief plant communities of Alberta, as these have been defined by recent investigators.

Delimitation of still smaller biotic areas is proposed by Strickland (1938) in a paper on the Diptera of Alberta. He recognizes and maps 21 " ecological areas " on the basis of original vegetation, present utilization (ranching, wheat-growing, irrigation), soil, elevation and precipitation. A few of these areas relate definitely to present land-use and therefore they appear somewhat unrealistic in terms of natural biota; but, nearly all conform quite well to current ecological views.

PRAIRIE (Steppe) VEGETATION

Mixed Prairie (*Stipa-Bouteloua* Association)

This grassland characterizes the brown soil zone and much of the dark-brown soil zone of southeastern Alberta. Clarke (1930), in his pioneer grazing-land studies, refers to the vegetation of the brown soil zone as a short-grass formation comprising two chief types which he designates *Bouteloua-Stipa-Koeleria* and *Agropyron-Poa* associations. Moss (1932) speaks of the same region as Southern Prairie and gives *Bouteloua gracilis, Stipa comata, Agropyron smithii* and *Koeleria gracilis* as the dominant species. The term " Short Grass " for the prairies of the brown soil zone was perpetuated by Clarke et al (1942) and others, while the grassland of the dark-brown soil zone was designated " Mixed Prairie ". It is generally agreed now that the " short grass " phases (dominated by *Bouteloua gracilis*) of the region are to be interpreted as edaphic climax or as disclimax. However, Hubbard (1950) is definitely of the opinion that a " Short Grass " formation should be recognized for much of the brown soil zone. From exclosure and soil texture studies, he concludes that prairie dominated by *Bouteloua gracilis* is not merely a disclimax caused by grazing. Coupland (1950), whose work is reviewed below, seems to have achieved a satisfactory classification.

Moss (1944) reports a "*Bouteloua-Stipa* Association" for the southwestern part of the dark-brown soil zone. On the assumption that *Stipa comata* is the climax species of the Mixed Prairie, Moss and Campbell (1947) refer to this grassland as the *Stipa comata* association. They draw a boundary line between this grassland and the *Festuca scabrella* association to the north and west. This line extends through the dark-brown soil zone and represents the ecotone between the two communities.

An extensive and thorough investigation of the Mixed Prairie in Canada has been carried out by Coupland (1950). Though most of Coupland's work was done in Saskatchewan, numerous studies were made in Alberta, and his main conclusions may be taken to apply to our region. According to Coupland, the Mixed Prairie or *Stipa-Bouteloua* association is dominated by six grass species, namely, *Stipa comata, S. spartea* var. *curtiseta, Bouteloua gracilis, Agropyron dasystachyum, A. smithii* and *Koeleria cristata,* while a seventh grass, *Muhlenbergia cuspidata,* is a dominant in eroded areas. Twelve other grass species and four sedges are also characteristic, though not ranking as dominants. The chief sedge is *Carex eleocharis.* Composites and legumes are the most abundantly represented families of dicotyledons. Leading forbs include *Artemisia frigida, Phlox hoodii, Malvastrum coccineum, Pulsatilla ludoviciana, Gutierrezia diversifolia, Sideranthus spinulosus, Chrysopsis villosa, Artemisia gnaphalodes,* and species of *Solidago* and *Potentilla.* Important shrubs are *Rosa arkansana* and *Artemisia cana.*

From analyses of data obtained by the point-transect method of sampling, Coupland recognizes six well-defined types in the mixed prairie. Five of these, ranked as faciations, are regarded as fully developed (climax) types, and the sixth (the *Agropyron-Muhlenbergia* facies) is subclimax as a result of erosion. The *Stipa-Bouteloua* faciation is the most extensive. It is the prevailing type on medium-textured soils upon glacial till deposits in the moister part of the brown soil zone and the drier part of the dark-brown soil zone. Approximately 60 per cent of the total vegetation of this grassland type is said to consist of three grasses, *Stipa comata, S. spartea* var. *curtiseta* and *Bouteloua gracilis,* though these occupy only 12.8 per cent of the soil surface. The vegetation is composed of three layers, the upper consisting of the culms of mid-

grasses and the flowering stalks of taller forbs, the middle layer characterized by *B. gracilis, Carex eleocharis* and certain shorter forbs, the lowermost being a mat of *Selaginella densa.* The *Bouteloua-Stipa* faciation occurs on areas of medium- to coarse-textured soil in the drier part of the brown soil zone, on areas of coarse-textured soil in the moister part of this zone and in exposed situations throughout the region. The *Stipa-Agropyron* faciation characterizes areas of higher moisture efficiency. The *Agropyron-Koeleria* faciation occurs on soils developed on uniform clay deposits occupying the beds of former glacial lakes. A variant of the latter faciation, with *Agropyron smithii* as the sole dominant, occurs on slightly alkaline clay flats and on certain alluviated clay flats. The *Bouteloua-Agropyron* faciation occupies clay loam, solonetzic soils particularly eroded patches (" burn-outs "), in the drier part of the brown soil zone in southwestern Saskatchewan. The cactus, *Opuntia polyacantha,* is widespread in this type, ranking next in abundance to *Artemisia frigida.* Whether the *Bouteloua-Agropyron* faciation is prevalent in Alberta appears somewhat uncertain. Coupland says that the solonetzic soils of southeastern Alberta are coarse-textured and support the *Bouteloua-Stipa* faciation. Solonetz soils in Alberta have been mapped and described by Odynsky (1945b), but the native vegetation associated with these soils awaits adequate study, especially in the northwestern part of the brown soil zone and extending northward through the dark-brown and black soil zones.

In the various climax faciations recognized by Coupland, grasses and sedges compose 84 to 95 per cent of the total basal area, the forbs and shrubs 5 to 16 per cent of the basal cover. A considerable portion of the entire mixed prairie has been modified by overgrazing. Vegetational changes caused by grazing have been adequately discussed by Clarke (1930), Clarke and Tisdale (1936), and Clarke et al. (1942). In general, overgrazing is said to have resulted in decreased vigor of the mid-grasses and of plants furnishing palatable browse. In dry locations a consocies of *Bouteloua gracilis* is the common indicater of overgrazing. Under severe grazing and trampling, *Carex eleocharis* gains in density at the expense of the grasses. For further information on the ecology of the mixed prairie in Canada, including significant observations on many of the leading species, Coupland's excellent monograph should be consulted.

MAIN PARKLAND PRAIRIE (*Festuca scabrella* Association)

This is the characteristic prairie of the black soil zone and aspen grove belt of southwestern and central Alberta. It extends eastward into Saskatchewan as a belt north of the Mixed Prairie. It is also the grassland of the parkland area on the plateau of the Cypress Hills in southeastern Alberta. The dominant species, *Festuca scabrella,* is properly described as a bunch grass; yet, in our region it appears generally to form short rhizomes that serve to enlarge the tussock. In the last edition of Hitchcock's (1950) Manual, this species is described as "rarely producing a slender rhizome". It may be noted here that some authorities treat *F. scabrella* as a sub-species or variety of *F. altaica* Trin.

HISTORICAL CONSIDERATIONS. Recognition of this grassland as a distinct and important type has come only recently, though the region covered is extensive and the dominant grass forms conspicuous tufts with long leaves and culms. Our observations indicate, however, that this species forms very few flowering stalks in some years. John Macoun (1882), usually a keen observer and accurate reporter, makes no mention of *Festuca scabrella* for our region; indeed, he seems to have confused this species with *Stipa spartea.* The latter he refers to as "northern buffalo grass". He says this is the famous grass of the hills in the Bow River country and forms the bulk of the winter pasture. He states, too, that as hay it is equally as good as grass, for, having produced next to no seed, the whole of the nutriment is laid up in the leaves. "It is not true of our Buffalo grass that the seed is among the leaves as it is in Kansas", writes Macoun. Evidently he was referring, at least in part, to *Festuca scabrella,* though there was surely considerable *Stipa spartea* var. *curtiseta* in the same grassland, and it is strange that the awns of that grass did not impress him. Failure to recognize the fescue (as such) may have been because of the paucity of culms formed by that grass in the seasons of Macoun's travels across the prairie. It seems likely that other observers have failed, for the same reason, to note the dominant role of this species. Macoun (1882) does recognize one of the chief tall dense grasses of the Cypress Hills plateau as a species of *Festuca.* Clarke (1930) reports *Festuca scabrella* as one of the leading grasses of benchlands in southern Alberta.

In a brief account of the parkland prairie (called Northern

Prairie) of south central Alberta, Moss (1932) reports *Festuca scabrella* as one of the chief grasses, along with *Koeleria gracilis, Agropyron* spp. and *Avena hookeri.* The dominance of *F. scabrella* in the grasslands of southwestern Alberta, the Cypress Hills, and portions of the park belt was recognized by Clarke et al. (1942) in their " submontane " type of mixed prairie, termed the *Festuca-Danthonia* association. The chief grasses are said to be *Festuca scabrella* (dominant), *Koeleria gracilis, Agropyron subsecundum, Danthonia parryi, D. intermedia* and *Festuca idahoensis.* For the southwestern black soil region of Alberta, a *Festuca-Danthonia* association, described by Moss (1944), further emphasized the significance of *Festuca scabrella* in our vegetation. According to Moss, the dominant grasses are *F. scabrella, F. idahoensis, Danthonia intermedia* and *D. parryi,* of which the *Danthonia* species are localized in their dominance, and *D. parryi* is largely restricted to the western part of the region. Characteristic associated grasses include *Koeleria gracilis, Agropyron griffithsii, A. dasystachyum, A. trachycaulum, Stipa spartea* var. *curtiseta, S. columbiana, Poa cusickii* and *Avena hookeri.* Listed also as members of this association are some 12 grasses of secondary importance, six sedges, seven shrubs and over 65 forbs. The association is discussed in various of its relationships, including the transition to the *Bouteloua-Stipa* association eastward, correlations with climatic data and with soil zones, the prairie-woodland ecotone, and affinities with the so-called " Northern Prairie " of the aspen grove belt to the north and northeast. The latter problem is considered more fully by Moss and Campbell (1947) in their treatment of the *Festuca scabrella* association as the climax grassland for the entire aspen parkland (Fig. 1).

CLIMAX GRASSLAND. The *Festuca scabrella* association is envisaged by Moss and Campbell as the climax grassland and also the virgin prairie of the parkland belt. A sharp distinction is drawn between this association, in which *Festuca scabrella* is the sole dominant, and fescue grassland produced by mowing for hay or by moderate to heavy grazing. The latter grassland shows a marked reduction in the fescue and an increase in secondary species, notably, *Agropyron trachycaulum* (including *A. subsecundum*), *Stipa spartea* var. *curtiseta, Koeleria cristata* (*K. gracilis*) *Agropyron dasystachyum, Danthonia* spp., *Carex* spp.

and certain forbs. Listed for the climax association are some 150 species of higher plants. Of these, about 125 are described as "characteristic" and 70 as "constant" members of the association. Many additional species are recorded for the modified fescue grassland. Some 50 species found in the southern portion of the association are not recorded for the north, while only four species in the north are not noted for the south. The richer flora of the southern part of the association is explained in terms of proximity to a variety of other vegetational types, especially of the mountains, and in terms of the time element, insufficient time having elapsed since glaciation for certain southern species to have reached the north. Of the grasses found only in the southern part (south of the Red Deer River), *Festuca idahoensis* and *Danthonia parryi* call for special mention, for these are the chief species associated with *Festuca scabrella* in the *Festuca-Danthonia* association described by Moss (1944). Inclusion of this association in the *Festuca scabrella* association by Moss and Campbell (1947) is based on the interpretation of *F. scabrella* as the climax dominant and the other two species as subclimax. Of particular interest is the role of *Danthonia parryi*. This grass is said to dominate in localized areas, especially on exposed, wind-swept slopes north of Waterton Lakes Park and in the Porcupine Hills, behaving as an edaphic subclimax species and as a disclimax under heavy utilization. According to a recent report by Hanson (1953), this grass is very prominent in the present condition of our ranges, especially in the Porcupine Hills, producing more forage there than any other single species. Hanson further reports that this species is replaced, in the mountain valleys to the west, by *Danthonia intermedia*, a smaller and less palatable species.

The *Festuca scabrella* association, as it occurs on the plateau of the Cypress Hills, has been described for the Saskatchewan portion of the Hills by Coupland and Brayshaw (1953) and by Breitung (1954) for both Saskatchewan and Alberta parts of the Hills. Coupland and Brayshaw report that the association occurs there on black soils, that there is an abundance of the shrub *Potentilla fruticosa*, and that the chief grasses are *Festuca scabrella* (dominant and occupying an average of 55 per cent of the non-shrubby cover in the sites sampled), *Agropyron subsecundum*, *Danthonia intermedia*, *Helictotrichon hookeri* (*Avena hookeri*)

and *Stipa spartea* var. *curtiseta,* while secondary grasses are *Koeleria cristata, Agropyron smithii, A. dasystachyum* and *Muhlenbergia richardsonis.* Breitung places the associated grasses in a somewhat different order of prevalence and gives a few others as being common, e.g., *Festuca idahoensis* and *Poa interior.* Common and conspicuous forbs include *Pulsatilla ludoviciana, Cerastium arvense, Achillea millefolium, Erigeron glabellus, Gaillardia aristata, Galium boreale, Lupinus argenteus* and *Hedysarum alpinum* var. *americanum.* Breitung says that two of the most striking features of this prairie are its color and luxuriance, the grassland in certain seasons becoming a veritable flower garden. Seventy years earlier Macoun (1882) wrote in similar vein as follows: " The grasses of the plateau are so tall that for miles at a time we had great difficulty in forcing our way through them . . ." and " In all my wanderings, I never saw any spot equal in beauty to the central plateau of the Cypress Hills ".

The fescue grassland of the aspen grove belt of western Saskatchewan, as described by Coupland and Brayshaw (1953), is similar to that already discussed for adjacent Alberta. The importance of *Festuca scabrella* varies from complete dominance in the northern fringe to co-dominance with *Stipa spartea* var. *curtiseta* in the northern part of the dark-brown soil zone. Throughout all of the black soil zone the fescue is much more abundant than *Stipa.* In Clementsian language, the fescue community is described as postclimax to the *Stipa-Agropyron* faciation of the mixed prairie, the latter commonly occuping exposed locations within the aspen grove region, such as south-facing slopes and tops of knolls; the fescue community is preclimax to aspen forest. The general appearance of this grassland is the same as in the Cypress Hills of Saskatchewan except for the absence of *Potentilla fruticosa.* Quantitative data are presented concerning the composition and structure of the grassland. On the basis of an analysis of these, it is concluded that the grassland of the Cypress Hills and the northern fringe of the aspen grove belt in Saskatchewan is part of the *Festuca scabrella* association as described by Moss and Campbell (1947). In these areas, which are characterized by the more moist black soils, *F. scabrella* occupies about 55 per cent of the basal cover provided by herbs. The principal subdominants are *Agropyron subsecundum, A. trachycaulum,*

Danthonia intermedia, Helictotrichon hookeri, Koeleria cristata, Muhlenbergia richardsonis, Stipa spartea var. *curtiseta* and *Carex* spp. The chief forbs are said to be *Cerastium arvense, Achillea millefolium, Galium boreale* and *Anemone patens.*

It is concluded by Coupland and Brayshaw that the *Festuca scabrella* community of Alberta and western Saskatchewan can not be considered to be allied to any of the six grassland associations previously described in North America (Weaver and Clements, 1938) and should therefore be considered as a seventh association of the grassland formation. The eastward extension of the *Festuca scabrella* association evidently requires further investigation. Coupland and Brayshaw say that they could not be certain that this type of vegetation is climax eastward of Saskatoon. Preliminary studies indicate that the ecotone between the fescue grassland and the true prairie to the southeast (Weaver and Fitzpatrick, 1934) is very wide and varied in composition.

The prairie vegetation of the park belt in Alberta and Saskatchewan is closely related to the grasslands of Idaho and other parts of the northwestern United States, and also to those of south-central British Columbia. This was pointed out by Clements and Clements (1939) in a brief discussion of " submontane " prairie. Important elements of the Palouse prairie of western Idaho and eastern Washington, notably, *Festuca idahoensis, Stipa columbiana, Agropyron spicatum, Lithospermum ruderale, Geranium viscosissimum* and *Balsamorhiza sagittata,* are said by Moss (1944) to extend into Alberta. Hanson (1953) emphasizes a floristic continuity from the Palouse prairie, through the valleys of British Columbia and mountain passes into Montana and southern Alberta, to the foothills of Alberta, supporting the theory that many of our species have moved in from the southwest along these routes. Of interest here is Tisdale's (1947) study of grasslands in the southern Interior of British Columbia. The three vegetational types recognized by Tisdale are linked by the chief dominant, *Agropyron spicatum,* into one major community. *Festuca scabrella* is reported as abundant and often co-dominant. In fact, the most mesic of the three grassland types is dominated by *A. spicatum* and *F. scabrella.* Tisdale states that the abundance of *F. scabrella* in southern British Columbia seems to link the grassland there with that of the foothills in Alberta.

PEACE RIVER PRAIRIE (*Agropyron-Stipa* Association)

This grassland is associated with poplar and willow groves to form parkland areas on dark soils in the generally forested Peace River region (Fig. 1). Earlier work on this vegetation by Raup (1934, 1935) and others is reviewed in a recent paper by Moss (1952). The grassland is described by Moss as an *Agropyron-Stipa-Carex* community, comprising three subtypes or faciations, viz., *Agropyron-Carex* on low areas, *Stipa* on dry slopes and *Agropyron-Stipa* on mesic sites. For the entire community 154 vascular species are recorded, and for the *Agropyron-Stipa* faciation, which is the most common prairie grassland of the region, 139 vascular species, consisting of 36 graminoids, 84 forbs and 19 woody species. This faciation is interpreted as the "climax" grassland of the region and accordingly might well be given the status of a plant association. On this interpretation the whole community may be designated the *Agropyron-Stipa* association. The chief grasses and sedges in the climax type are *Agropyron trachycaulum* (including *A. subsecundum*), *Stipa spartea* var. *curtiseta, Koeleria cristata, Stipa richardsoni, Carex obtusata* and *C. praticola.* Leading forbs are *Galium boreale, Achillea millefolium, Thalictrum venulosum, Geum triflorum* and *Solidago* spp. Common shrubs are *Symphoricarpos* spp., *Rosa* spp. and *Amelanchier alnifolia.* Characteristic species of the *Agropyron-Carex* faciation of low moist areas include *Agropyron trachycaulum, Carex atherodes, Schizachne purpurascens, Bromus* spp., *Calamagrostis* spp., *Hierochloe odorata, Carex praticola* and *Vicia americana.* The sharply contrasting *Stipa* faciation of xeric situations, such as river valley slopes, includes *Stipa spartea* var. *curtiseta, Stipa columbiana, Agropyron dasytachyum, Koeleria cristata, Artemisia frigida* and *Pulsatilla ludoviciana.* The presence of a cactus, *Opuntia fragilis,* on these dry slopes and at a latitude 56° is of some interest. Worthy of note is the absence of *Bouteloua gracilis* and *Stipa comata,* common grasses of similar habitats in south-central Alberta.

The *Agropyron-Carex* faciation has evidently succeeded a marsh community characterized by coarse grasses and sedges, including *Calamagrostis inexpansa* and *Carex atherodes.* These prominent members of this faciation are interpreted as relict species that have persisted from the lower community. Upon further drying of the

lowland areas the *Agropyron-Carex* faciation develops into the climax *Agropyron-Stipa* type. The *Stipa* faciation of xeric areas may be followed by the climax type as these areas become more mesic through gradual levelling of the terrain. Evidence is presented by Moss that the *Agropyron-Stipa* grassland is not the climatic climax vegetation of the region, but instead an edaphic climax. There is a marked tendency for willow and poplar to encroach upon the grassland areas; but succession to forest has long been effectively retarded by fires and by special physiographic and edaphic features of these areas, notably poorly drained and inadequately aerated soils.

The Peace River grassland as described by Moss (1952) is evidently closely related to the prairies described by Raup (1935) for Wood Buffalo Park in northeastern Alberta and northward. The relationship between these grasslands and those of the arctic tundra constitutes "one of the most intriguing problems of the north" (Raup, 1941). The Peace River grassland has rather close floristic affinities with the *Festuca scabrella* association. Its climax type is dominated by the leading secondary species in the fescue grassland, namely, *Agropyron trachycaulum, Koeleria cristata* and *Stipa spartea* var. *curtiseta;* but there is one outstanding difference, viz., the absence of *Festuca scabrella,* the dominant species of the fescue association. It seems, therefore, that the Peace River prairies can not be included in the *Festuca scabrella* association, which Coupland and Brayshaw (1953) have proposed as a seventh association in the grassland formation of North America. Nor can the Peace River prairies be classified as part of the Mixed Prairie association because of the absence of such grasses as *Bouteloua gracilis* and *Stipa comata.* It is suggested, therefore, that the *Agropyron-Stipa* association of the Peace River region might be considered as an eighth association in the grassland formation of North America.

PARKLAND (Grove Belt)

Grassland-Woodland Ecotone

Typical parkland may be described as a mosaic of prairie patches and aspen groves, with prairie occupying the drier situations and aspen the more moist and sheltered places. The main parkland extends as a fringe along the foothills of southern Alberta and

northeastward as a broad belt across the south-central part of the Province to the Saskatchewan border. Smaller isolated parkland areas occur in the Cypress Hills, the Hand Hills, and in the general Peace River region (Fig. 1). Transition from parkland, whether to open prairie or to forest, is usually gradual. The following account of our main parkland, written nearly a century ago, is quoted here as an important early report and as a description that applies even to-day to relatively undisturbed portions of our parkland: "In this district the woods are very scanty and consist almost exclusively of aspen poplar, which form small groves and artificial-looking clumps that dot the rich pasture lands" and "As the country towards the south merges into the open prairie, the clumps of copse and young poplars are found only nestling on northern exposures. The last outliers of the woods to the south generally consist of 'islands', as they are called, which make a show from a distance, but when approached are found to consist of small species of willow" (Palliser, 1863).

The parkland, as a transition or tension belt, actually comprises thousands of true tension lines or ecotones, these occurring where aspen and prairie communities meet (Moss, 1932). Such ecotones consist of representatives of the two competing communities, including certain grasses and shrubs, notably *Symphoricarpos occidentalis*. In some situations the aspen invades the grassland by extending its roots and forming suckers that establish there as trees. This tendency for aspen to invade and replace prairie vegetation has been reported for different parts of the parkland (Moss, 1932, 1944, 1952). Counteracting this tendency are various agencies, such as burning, grazing, damage by rabbits, and desiccating winds. The extent to which poplars reproduce by seed and establish new stands in the parkland and prairie regions is problematical. At some time in the past, either in comparatively recent years or many centuries ago, the thousands of isolated aspen groves of the parkland must have been initiated by seed. Various aspects of this problem have been discussed by Moss (1932). The question of the transfer of viable seed and the establishment of seedlings was investigated by Moss (1938) for our region. Longevity of poplar seeds under natural conditions is from two to four weeks, and establishment of the seedlings occurs only when the surface layer of the soil is continuously moist during at least

the first week of their growth. This is said to be due to the slow growth into the soil of the primary root and also to absorption being largely dependent upon a brush of delicate hairs near the soil surface. It seems, therefore, that new poplar groves are likely to arise in our region under rather exceptional climatic conditions.

Explanations of the origin and persistence of prairies, especially where there is evidence of current or former woodland invasion, are of perennial interest. Some of the early explorers evidently believed that our parkland prairies were originally well forested. Palliser (1863) reports the region south of the Battle River and north of the Neutral Hills, near the Alberta-Saskatchewan border, as old forest land with good soil, the forest having been destroyed by fire and the region now dotted with small poplar clumps. According to Palliser, that portion of fertile country lying between his "triangle" (the Canadian extension of the central American desert having for its base the 49th parallel from longitude 100° to 114° W., with its apex reaching to the 52nd parallel of latitude) and the present forest to the north was once heavily timbered. It was thought to contain a large spruce element, for Palliser's Report reads: "Sometimes a small clump of the spruce fir has been left by the fire" and "From Fort Carlton to Edmonton, a distance of nearly 400 miles, there were not more than five or six spots where any of the coniferae were left". Dawson (1879) reports that there can be no doubt that the prairies of the Peace River have been produced and are maintained by fires. It seems to have been assumed by many early writers, also by pioneer settlers, that the Indians set fires for the express purpose of maintaining the grassland. These earlier ideas have tended to prevail, along with another popular belief that the buffalo (bison) had an important part in maintaining the prairies. The "master hand of climate", especially the precipitation-evaporation factor, has been increasingly emphasized by investigators (Borchert, 1950). This writer makes the trenchant comment that "Grassland climates favor fire, just as they favor grass whether there are fires or not".

Burning has doubtless been very effective in counteracting natural succession to woodland in the days of the Indians and buffalo as well as more recently. Where settlers have operated to prevent fires, the woodland has often extended at the expense of the prairie. For the parkland regions of Alberta, the importance

of the pyric factor has been emphasized by Moss (1932, 1952, 1953a), also by Moss and Campbell (1947). But these authors, like several other recent investigators of prairies, point to additional aspects of the problem. They agree with Borchert (1950) as to the "master hand" played by climate. Moreover, like Borchert and others, they realize the significance, not only of prevailing conditions but also of major climatic shifts of the past, as revealed by evidence from soil profiles, peat pollens and relict vegetation. For example, the degraded black soils presently found on the forested fringes of our main parkland are thought to have been formed under grassland. Thus various lines of evidence suggest the theory of a xerothermic period, a late post-glacial, prehistoric period, with more frequent and prolonged drought conditions than currently prevail in our grassland regions. This period is believed to have seen considerable extension of prairies. At the end of the xerothermic period and the return of somewhat cooler and more humid conditions, the adjacent forest began slowly to invade the grasslands, being more or less retarded, however, by the pyric and biotic factors already discussed. Indeed, prairie has tended to persist on hot dry situations, such as south-facing slopes, especially where these are swept by drying winds. Even today, prairie species occur as relicts on dry slopes in the northern forest, far beyond the main parkland regions. Other examples of physiographic and edaphic factors making for the persistence of prairies in localized areas have already been mentioned in this review. It should be noted in passing that more than one prolonged warm dry period may have occurred during postglacial time. Even in historical times a dry cycle, 400 to 1100 A.D., is said to have occurred (McComb and Loomis, 1944). During this period there may have been a temporary set-back to tree invasion and some return of woodland to prairie.

Of special interest here are the prairies of northwestern Alberta. The suggestion has been made (Moss, 1952) that the existing prairie patches of that region, especially the drier of these, might well be interpreted as remnants of a very extensive grassland which occupied much of the region during the xerothermic period and might even have been connected with the main parkland of south-central Alberta. The numerous floristic elements common to the Peace River and more southern prairies suggest a community of

origin for these grasslands. This hypothesis finds support in the recent work of Hansen on pollen analysis of peat sections in Alberta. Indeed, Hansen (1949) suggests that the Peace River grasslands may be relicts of a postglacial expansion of prairie "during a warm, dry maximum between 8,000 and 4,000 years ago". On the other hand, Raup (1934, 1935) sees no need to postulate a warm-dry segment of time for the boreal region and envisages only a gradual amelioration of the climate since glaciation. He stresses the probability of a fairly short postglacial period for the introduction and establishment of vegetation in the region. During this period our northern grasslands may have developed from tundra through subarctic grass-sedge stages. The strong *Carex* element in the Peace River grasslands may be significant in this connection.

These interrelated phytogeographical problems will doubtless be clarified through further study of peat profiles and of subarctic "prairies" (Moss, 1952). Possibly our main parkland prairie followed the coniferous forest north in the xerothermic period, while the prairies of northern Alberta and adjacent regions developed, at least in part, from subarctic grasses and sedges. The absence of *Festuca scabrella* from the northern prairies may be significant in this connection. These considerations suggest to the reviewer still another aspect of the parkland-prairie enigma, viz., various effects of the availability of species for establishment in different areas. For example, would the main Peace River grassland be characterized by *Festuca scabrella* had that species reached the region centuries ago?

Grassland and Soils

Various aspects of grassland in relation to climate and soils have been mentioned earlier in this review. Of some interest in connection with the development of grassland soils is a suggestion put forward by Moss and Campbell (1947). They support the view generally held by students of climate-soil-vegetation relationships in steppe-woodland regions, that black or chernozem soils are essentially grassland soils developed through many centuries in a cool continental climate of moderate rainfall; that the steppe or prairie areas, likewise the black soil areas, were originally larger than now, and have been invaded by forest rather recently in soil

history; that the black soils thus covered by forest have been modified by podsolization to become degraded or transition (grey-black) soils. Emphasizing their conclusion that the natural vegetation of the black soil and grey-black soil zones of our main parkland was through many centuries a *Festuca scabrella* association, in which a single species predominated, and assuming that most of the organic matter in prairie soils has derived directly or indirectly from the roots and crowns of grasses, these authors conclude that the bulk of the organic substance in the black soils was produced by the dominant grass species, *Festuca scabrella.* Even in the dark-brown soil zone, this grass seems to have flourished to some extent and no doubt has furnished that soil with much organic material.

It is suggested, therefore, that a large proportion of the agricultural wealth represented by the black and related soils of Alberta had its origin in the activity of just one kind of higher plant. This claim may appear slightly exaggerated, especially when one considers the possibility of certain other grasses having dominated in earlier stages of the grassland's history, also the possibility of other grasses having been abundant under buffalo grazing, and moreover, when one thinks of various associated shrubs and forbs, especially the legumes, which may have been more prevalent in the virgin prairie than they are today. In any event it is worthy of note that the organic matter of our black soils has derived from quite a different primary source (in terms of main plant species) than that of either the dark soils of the Peace River prairies or the brown soil of southeastern Alberta.

FOREST VEGETATION

Poplar (*Populus*) Association

Of the six species of poplar native to Alberta, four are confined to southern and southwestern regions, where they occur mainly in river and stream valleys. These will be considered later in this review. Two of the species, the aspen or white poplar (*Populus tremuloides*) and the balsam or black poplar (*P. balsamifera* = *P. tacamahacca*), are widespread in the Province, comprising extensive pure stands and also being associated with other tree species, on many kinds of terrain. The aspen occurs over a wide range of edaphic conditions, including dry knolls, moist river flats

and such soils as loam, clay and sandy. The balsam poplar is more restricted in its occurrence, reaching its best development in the more moist situations, such as river flats (Moss, 1932). While these species are found throughout the forest regions of Alberta, their greatest concentration is in the south-central part, adjacent to the main parkland (Halliday and Brown, 1943). Northward and westward, poplar tends to be replaced by conifers. As already indicated in this review, aspen is the characteristic tree of parkland areas. Moreover, it is regarded as the climax species of the main parkland of Alberta (Moss, 1932), as also of corresponding parts of Manitoba and Saskatchewan (Bird, 1930).

The entire poplar vegetation of central and northern Alberta is regarded as an association, within which aspen and balsam poplar consociations are recognized (Moss, 1932, 1953a). Poplar stands are usually even-aged; this is explained by the fact that the trees of a stand start as suckers after a complete burning off of the parent stand. The aspen rarely exceeds 120 years in age, the balsam poplar 135 years. For the poplar association in central Alberta somewhat over 200 plant species are cited, of which only about 50 vascular plants and a very few mosses are regarded as important constituents. For the community in northwestern Alberta, somewhat similar records have been published and certain minor floristic differences noted.

Typically, the poplar association consists of five strata: (*a*) taller trees, forming a nearly continuous canopy; (*b*) smaller trees and larger shrubs, an intermittent layer, usually poorly developed in the aspen consociation; (*c*) lower shrub layer, rich or sparse, and more or less obscured in summer by the next stratum; (*d*) taller herbs, often an almost continuous stratum and quite prominent in the latter part of the growing season; (*e*) lower herbs, including mosses and lichens, forming a carpet which locally is continuous, especially in the balsam poplar consociation. Bands of mosses, especially *Pylaisia polyantha,* are common on tree trunk bases.

Characteristic species of the balsam poplar consociation include: the dominant tree, *P. balsamifera;* the shrubs, *Cornus stolonifera, Ribes* spp. and *Lonicera involucrata;* the herbs, *Mertensia paniculata, Equisetum* spp. and *Petasites palmatus;* and the mosses, *Hylocomium splendens* and *Aulacomnium palustre.* Characteristic

species of the aspen consociation include: the dominant tree, *P. tremuloides;* the shrubs, *Symphoricarpos albus, Amelanchier alnifolia* and *Shepherdia canadensis;* and the herbs, *Cornus canadensis* and *Maianthemum canadense.* Prominent in both consociations are: the shrubs and small trees, *Rosa woodsii, R. acicularis, Viburnum edule, Rubus idaeus* and *Salix* spp.; the herbs, *Rubus pubescens, Aster ciliolatus, Vicia americana, Lathyrus ochroleucus, Pyrola asarifolia, Fragaria glauca, Galium boreale, Epilobium angustifolium, Viola rugulosa, Thalictrum venulosum, Calamagrostis canadensis* and *Agropyron trachycaulum;* and the mosses, *Pylaisia polyantha* and *Mnium cuspidatum.* Certain leading species of the poplar association in central Alberta, notably *Corylus cornuta, Prunus* spp., *Aralia nudicaulis* and *Disporum trachycarpum,* are said to be much less common in northwestern Alberta. On the other hand, the poplar community of the latter region includes a few Cordilleran species not listed by Moss (1932) for central Alberta, e.g., *Salix scouleriana, Spiraea lucida, Arnica cordifolia, Arctostaphylos rubra* and *Castilleja raupii.* It may be noted here, however, that Turner (1947) has reported the first two of these species, as well as several other Cordilleran species, near Pigeon Lake, more than 100 miles east of the Rocky Mountains in south-central Alberta.

The poplar vegetation of the Rocky Mountain region of Alberta has received relatively little study. The aspen poplar consociation of the parkland and outer mountains in southwestern Alberta has been described briefly by Moss (1944). Aspen groves of this region are said to be generally of low stature for their age, growth in height having been retarded by the prevailing winds. Those in the more exposed positions have truncated tops and the characteristic wind-blown habit. This community is compared with the aspen consociation of central Alberta and found to be sufficiently alike in physiognomy, internal structure and floristic composition to be classified as a variant of the same aspen consociation. Minor floristic differences are noted, including the presence in the south of such Cordilleran species as *Rubus parviflorus* and *Spiraea lucida.*

The aspen poplar woods of the Cypress Hills have been described briefly by Breitung (1954). These woods occur chiefly on the northern slopes of the Hills and along the lower edge of the pine

forest. Groves on exposed sites are stunted and low in stature, with "branchy", wind-blown crowns, caused by strong, desiccating winds. Available information indicates that this vegetation may be treated as a variant of the aspen consociation, being most closely related to the phase of this consociation in southwestern Alberta. Cordilleran species prominent in the aspen community of the Cypress Hills include *Salix scouleriana, Bromus marginatus* and *Elymus glaucus.*

Effects of Burning

A poplar stand that has been burned off is usually soon replaced by a dense growth of young trees, with only a temporary alteration in the associated vegetation. Certain species, including *Epilobium angustifolium, Aster* spp. and some of the shrubs and grasses, become quite prominent; but, after two or three years, these are suppressed by the young poplars and there is a gradual return to the original composition of the community. Cutting of poplar stands produces essentially the same results (Moss, 1932).

Fireweed, *Epilobium angustifolium,* is a striking feature on burned forest areas in our region. A study of the ecology of this species by Moss (1936) revealed facts bearing upon its abundance on burned land, and led to the discovery of an interesting anatomical character, namely, rings of cork in the wood of the underground organs. The sudden appearance of fireweed, generally attributed to wide dissemination of an abundance of seed, is explained in terms of proliferation of shoots from old deep-seated roots and rhizomes. Interxylary cork may relate to the persistence of these organs. Incidentally this discovery of internal cork in fireweed led to the finding of rings of cork in the wood of certain other plants, notably a species of *Artemisia* (Moss, 1934). Later reports of this structure (Diettert, 1938; Moss, 1940; Moss and Gorham, 1953) include discussions of its adaptational aspects in sage-brushes (*Artemisia* spp.) and various other plants.

Succession to Spruce

Natural succession of poplar to white spruce (*Picea glauca*) is clearly indicated throughout central and northern Alberta. Ecesis of spruce occurs in poplar stands of various ages, where seed is available, and under appropriate ground conditions. The young spruce grow slowly for many years; but as the poplar thins out

with advancing age the suppressed spruce come to overtop the poplar. This tendency of the spruce to supersede poplar is counteracted by biotic and pyric factors. Considerable damage is done to young spruce by snowshoe rabbits and other animals, but periodic burning is the major factor operating against succession to spruce. While a severe burn gives only a temporary setback to the sucker-regenerating poplar, it is devastating in its effects on spruce (Moss, 1953a). Poplar in relation to other forest vegetation will be discussed later in this review. Invasion of prairies by aspen poplar has been considered above.

BOREAL (NORTHERN) FOREST

White Spruce (*Picea glauca*) Vegetation

The white spruce of Alberta is generally reported as *Picea glauca* var. *albertiana*. However, there is considerable evidence that typical *Picea glauca* occurs also and that it merges with the variety in some parts of the Province. Until further study has been given to this taxonomic problem, the designation *Picea glauca* seems preferable. White spruce is the leading species of the Boreal Forest and Boreal-Cordilleran Transition regions (Fig. 1), if not in actual coverage, at least as the potential dominant. To a limited extent, it extends into the Subalpine and Montane Forest regions, where it grows at the lower elevations. In these regions, and also in the higher foothills, it merges with Engelmann spruce (*Picea engelmanni*). Where these species grow together, intermediates (hybrids) between them are said to be quite common. White spruce also occurs in the Cypress Hills.

Picea glauca association. This has been recognized as the chief type of white spruce vegetation in Alberta. For central Alberta this association is described briefly by Moss (1932). It is commonly found in habitats similar to those occupied by the balsam poplar consociation and has many species in common with that consociation. The associated trees and shrubs are rather few and sparsely scattered. They include *Populus balsamifera, Cornus stolonifera, Viburnum edule* and species of *Salix, Ribes* and *Rosa*. The herbaceous and moss flora is variable and generally patchy. Where the spruce forms a close canopy, there is usually a continuous ground cover of various mosses, chiefly *Hylocomium splendens, Hypum schreberi* and *Ptilium crista-castrensis*. Where

the stand is more open, this characteristic " feather moss " stratum is not so well developed, and certain herbs are often abundant there; these include *Linnaea borealis* var. *americana, Equisetum* spp., *Calamagrostis canadensis, Cornus canadensis, Mitella nuda, Rubus pubescens* and *Pyrola* spp. White spruce is said to be the natural successor to balsam and aspen poplar and to behave as the climax species of the region.

The white spruce vegetation is said to extend into northwestern Alberta, where it has been described by Moss (1953a) and interpreted as the climax forest vegetation for mesic sites there. Of four variants (faciations) of the association described by Moss, two are said to be prevalent: (*a*) *shrub-herb faciation:* the spruce generally not crowded; usually a strong admixture of poplars and the willow, *Salix bebbiana;* a prominent shrub stratum with *Viburnum edule, Ribes* spp. and *Rosa* spp.; and luxuriant herb strata with *Linnaea borealis* var. *americana, Rubus pubescens, Mertensia paniculata, Fragaria* spp., *Pyrola* spp., *Epilobium angustifolium, Calamagrostis canadensis, Cornus canadensis, Mitella nuda, Viola renifolia* and *Petasites palmatus.* (*b*) *feather moss faciation:* the spruce forming a fairly close canopy; shrubs and herbs relatively few and sparse; an almost continuous carpet of *Hylocomium splendens, Calliergonella* (*Hypnum*) *schreberi* and other mosses, with associated horsetails (*Equisetum* spp.), bunchberry (*Cornus canadensis*) and other species. These and other faciations of the association intergrade to form various mixtures, depending upon the terrain, the age and density of the spruce, and the past history of the area, especially in terms of burning. The feather moss faciation is regarded as the association climax, for, in the absence of burning the other faciations tend to develop into this type, the spruce gradually supplanting the shorter-lived poplar and birch, while most of the shrubs and herbs are replaced by mosses. " On the other hand, it seems doubtful whether this community is self-perpetuating as such, either following burning or subsequent to old age and decadence of the spruce" (Moss, 1953a).

The white spruce forests of northeastern Alberta and adjacent Mackenzie region have been described by Raup (1933a, 1946). Three divisions of these forests are distinguished, namely, flood plain spruce, upland mesophytic spruce, and parklike white spruce.

The first two of these types appear to be similar to the white spruce association of northwestern and central Alberta, the flood plain type being somewhat like the shrub-herb faciation described above, and the upland mesophytic type resembling the feather moss faciation. The subject of retrogression of spruce to poplar and pine following various kinds of forest fires and subsequent return to spruce has been well described by Raup (1946) for northern regions.

The white spruce forests of the foothills and mountains of Alberta have been given relatively little study. Recent reports by Bloomberg (1950) and Horton (1954) will be discussed later in connection with Cordilleran forests. For the Carbondale River area, in the mountains of southwestern Alberta and falling within the Montane Forest region, Cormack (1949) describes the virgin spruce forest, in which white spruce is thought to be the dominant species. However, since alpine fir (*Abies lasiocarpa*) is reported as common in the virgin stands and since many other Cordilleran and Montane elements are indicated, this forest, too, will be discussed under a later heading.

A brief account of the white spruce forest in the Cypress Hills by Breitung (1954) indicates that this forest might well be classified as a variation of the *Picea glauca* association of Alberta. Though closely associated with lodgepole pine stands and despite a few Cordilleran elements, this forest seems to resemble more closely the white spruce association of central and northern Alberta than spruce forests of the mountain region.

PARKLIKE WHITE SPRUCE FOREST. As noted above, this is one of three divisions of the white spruce forests described by Raup for northeastern Alberta. There it occurs mainly on high sand ridges, stony beaches and dune habitats near Lake Athabasca. It consists of open parklike stands with little or no undergrowth but often with a ground cover of fruticose lichens and mat-forming shrubs. The drier phase of this forest, as it occurs on sand, is somewhat like the white spruce vegetation described by Moss (1932) for a sandhill area near Edmonton in south-central Alberta, though differing markedly in floristic composition. Raup (1946) discusses the bearing of habitat, climate and species history on some of the anomalies of parklike spruce and jackpine forests in northern regions.

SUCCESSIONAL RELATIONSHIPS. White spruce is generally considered the climax species in vast areas of central and northern Alberta, as well as in parts of the foothills and lower mountain valleys. Succession of pine and other coniferous vegetation to spruce will be considered later. Here further attention is given to poplar-spruce relationships. Many observers have reported ecesis of white spruce in poplar stands and succession to spruce. White (1915), for example, points out that aspen makes an excellent nursetree for the spruce and claims that if fires are controlled the poplar will gradually be replaced by spruce. In a poplar stand, young spruce usually grow slowly for many years, apparently because of shading by the poplar. But, as the poplar thins out with advancing age, the suppressed spruce grow rapidly and may eventually over-top the remaining poplar. This situation is often met with in poplar stands of 70 years and older (Moss, 1932). Thus the white spruce may succeed the poplar; and under the dense shade of the spruce the characteristic subsidiary species of the white spruce association gradually replace those of the poplar community.

The severity of a burn has a profound influence on the subsequent forest, due to the differences in the habit of reproduction of the poplar and spruce. "Light fires, which merely burn over the top of the humus layer, stimulate suckering of aspen and encourage a vigorous growth of perennial minor species (shrubs and herbs) on the forest floor. Spruce is dependent on small seed for its regeneration, therefore it finds the above conditions of severe competition unfavorable for establishment. The result is generally the development of a pure poplar stand. On the other hand intense fires, by consuming the entire humus layer, simultaneously reduce the vigor of the aspen suckers, eliminate most of the minor vegetation and expose mineral soil, making possible the rapid invasion of spruce,—provided always that seed is blown in and subsequent climatic conditions are favorable. In the latter eventuality, a spruce stand with scattered poplar is likely to result". (Rowe, 1953). Proximity of parent trees as a seed source has been generally recognized as crucial. Spruce trees do not produce seed in quantity until they are at least 35 years old, and generally not until 45 to 60 years old. Therefore recurring fires have the effect of eliminating the spruce and maintaining poplar forest. As al-

ready stated, this actually is the situation in vast areas of central Alberta for which white spruce is the potential dominant.

However, setting aside the effects of periodic burning and assuming a spruce seed source, there still remains some doubt about the extent of spruce reproduction in poplar stands. This problem of spruce regeneration is now receiving critical study. Rowe (1953), in a discussion which emphasizes the complexity of forest site and the importance of giving due recognition to site as an " ecosystem ", makes an interesting comment on the conditions affecting establishment of spruce in poplar stands. He draws attention to the mechanical action of accumulating litter on plants of the forest floor, and reports that " field observations have shown that much of the mortality of the initially small spruce seedlings under hardwood and mixedwood stands can be attributed directly to smothering by poplar leaves ". Another aspect of white spruce reproduction, that of mechanical disturbance of the forest floor, is being studied in forests of the Rocky Mountains by Crossley (1952).

The fate of the so-called white spruce climax, in the form of old decadent stands that remain unburned, is also problematical. In general, it seems that young spruce do not root at all well in the moss stratum and deep duff of old spruce stands but that there is often considerable reproduction on decaying logs and stumps. This problem will be discussed further in connection with our review of Cordilleran forests.

Bog Forests and Bogs

The pioneer work on peat bogs in Alberta by Lewis and Dowding (1926) deals with the structure, vegetation, peat and history of small bogs (muskegs) in the vicinity of Edmonton and points to several problems presented by these bogs. Formed on fine glacial clay in small basins in morainic areas, these bogs are characterized by *Sphagnum* moss, with black spruce (*Picea mariana*) as the dominant tree and Labrador tea (*Ledum groenlandicum*) the leading shrub. However, *Sphagnum* is tending to disappear and to be replaced by vegetation indicative of drier conditions. Desiccation is caused at least partly by fires. Retrogression due to inflow of springs highly charged with mineral matter to form calcareous lakes in a peat basin is also reported.

Further studies reported by Lewis et al. (1928) deal with *Sphagnum* and birch bogs, bog forests, low-moors (cariceta) and reed-swamps of central Alberta, in various of their inter-relationships. The main results of these studies will be discussed below in relation to more recent investigations. The reports by Raup (1935, 1946) of bog vegetation in northeastern Alberta will be similarly related. Papers by Hansen (1949a, 1949b, 1952), though dealing mainly with pollen analyses of Alberta peats, contain valuable information on bog depths, nature of the peats, surface features and general bog development. The main conclusions based on peat pollens are presented elsewhere in this review.

Picea mariana ASSOCIATIONS. Forests dominated by black spruce exhibit a number of phases and intergrade with certain other kinds of vegetation. Two main types are recognized in northern Alberta; (*a*) black spruce–feather moss association, which intergrades locally with the white spruce association; (*b*) black spruce–bog moss association, regarded as a sub-climax stage of a *Sphagnum* bog sere (Moss, 1953b). "Though these associations have many species in common, including the same dominant, they do show significant differences in floristic composition; moreover, they are unlike in respect to internal structure and generally in substratum, origin, and development".

The black spruce–feather moss (*Picea mariana–Hylocomium splendens*) association is frequently accompanied by white spruce, aspen and willows. The floor is carpeted with "feather" mosses. Associated species include lichens (*Peltigera aphthosa* and *Cladonia* spp.), *Ledum groenlandicum, Vaccinium vitis-idaea* var. *minus, Rosa* spp., *Ribes* spp., *Equisetum* spp., *Cornus canadensis, Petasites palmatus, Linnaea borealis* var. *americana, Mitella nuda, Rubus pubescens* and *Carex* spp. This association seems generally to have developed on shallow depressions or on level terrain through sedge-grass-willow stages and without much peat formation. It is similar floristically to the "mature bog forest" described for central Alberta by Lewis et al. (1928), and somewhat like the dry phase of the bog forest reported by Raup (1946) for northeastern Alberta. Moss suggests that the black spruce-feather moss association may be interpreted as an edaphic climax, being long maintained as such by poor drainage and also by periodic burning.

The black spruce–peat moss (*Picea mariana–Sphagnum*) association frequently has tamarack, paper birch and certain willows associated with the spruce. The floor is characterized by bog mosses, especially *Sphagnum* spp., and by *Cladonia* spp. The chief flowering plants are *Ledum groenlandicum, Vaccinium vitis-idaea* var. *minus, Rubus chamaemorus* and *Smilacina trifolia.* The most striking structural feature is the uneven floor of *Sphagnum* mounds and the nearly continuous cover of Labrador tea. This association has arisen in depressions through acid bog stages and with the production of a considerable thickness of *Sphagnum* peat. It is interpreted as a subclimax community, maintained as such by prevailing edaphic conditions and by periodic burning. Natural succession is to a black spruce–feather moss community; but this trend is quite generally off-set by burning which causes retrogression to earlier stages of the bog forest sere. The "young bog forest" reported by Lewis et al. (1928) for central Alberta is essentially the black spruce–bog moss association, and the wet phase of the bog forest described by Raup (1946) for the Athabasca–Great Slave Lake region is similar to this association.

Black spruce vegetation, related to the black spruce–feather moss association, is known to occur in the foothills and on the lower mountain slopes of west-central Alberta. This has been described by Horton (1954) and will be discussed in our review of Cordilleran forests. In the more northern parts of Alberta, black spruce is known to occur apart from the two associations already described (Moss, 1953a). It grows there intermixed with pine and other tree species on several kinds of terrain. On the upper slopes of the Caribou Mountains, black spruce stands and also black spruce–lodgepole pine mixtures are reported by Moss and by Raup (1946).

Drepanocladus-Carex AND *Sphagnum* BOGS. Open bogs, characterized by sparse tree cover, are of various kinds and present a number of complex problems. According to Moss (1953b), the bogs of our region fall into two main series: (*a*) *Drepanocladus-Carex* bogs, formed in basins from aquatic vegetation and marsh, and leading through bog willow and bog birch stages to a *Larix laricina* association, or through various stages to *Sphagnum-Ledum-Picea* vegetation; (*b*) *Sphagnum* bogs, developed as just indicated or from aquatic-marsh vegetation without the interpola-

tion of marked *Drepanocladus* or shrub phases. The latter mode of succession to *Sphagnum* bog has probably been the chief mode of bog development in Alberta, especially northward. However, further investigation is needed on this as on many other aspects of our bogs. As already indicated, open bogs tend to develop into bog forest—the *Picea mariana–Sphagnum* association. When a bog forest is burned there is retrogression to earlier stages of the bog sere. Certain of our open bogs, or portions of bogs, represent disclimax conditions brought about mainly through burning. Repeated burning of relatively mature *Sphagnum* bogs tends to produce an open bog phase which is more or less static. This is the *Ledum* moor of Lewis et al. (1928) and is characterized by Labrador tea, *Polytrichum, Cladonia,* low mounds of *Sphagnum fuscum, Eriophorum spissum, Vaccinium* spp. and scattered black spruce, paper birch and willows.

Sphagnum SUCCESSION AND THE REGENERATION CYCLE. The ecological relationships of various species of *Sphagnum* in Alberta bogs have been discussed by Marion Moss (1949) and Moss (1953b). In terms of leading sphagnums, succession from the early aquatic condition, through intermediate stages, to the final "xeric" stage may be shown as follows: *Sphagnum subsecundum* (or, *S. teres*) → *S. recurvum* → *S. magellanicum* → *S. capillaceum* → *S. fuscum.* Northward in the region, *S. magellanicum* is said to be rarely represented in the sere. This sere is clearly seen in large wet depressions of bogs, and also where sphagnum is advancing upon marsh or *Drepanocladus* bog.

The "Regeneration Complex", described by various European writers, has been discussed for Alberta bogs by Moss (1953b). This is the condition of a growing sphagnum bog where the majority of the hummocks are covered by the more xerophilous (or, less hygrophilous) species of the sere, and where the hollows are occupied by relatively hygrophilous species. The aspect is a mosaic of hummocks and hollows occupied by different species, and the development is cyclic, the hollows becoming the sites of mounds, and the mounds the sites of hollows, through a series of *Sphagnum* sequences. The state of dynamic equilibrium inherent in the cycle is followed, sooner or later, by a condition of static equilibrium, viz., when the general surface of the bog has become

too dry for any of the sphagnums except *S. fuscum.* It is to be noted that the " Regeneration Complex " shows the same sequence of sphagnums as in the *Sphagnum* sere, except that the strictly aquatic species do not occur in the former.

Larix laricina ASSOCIATION. This type of vegetation, recognized some years ago in central Alberta by Lewis et al. (1928), has been described recently for more northern areas by Moss (1953b). Structurally the association has a single tree dominant, the tamarack (larch), often with black spruce interspersed; a shrub layer, usually of bog birch and willows; an uneven floor with scattered pools and with wet, mossy mats or mounds; associated with the mosses, low, creeping shrubs (*Vaccinium* spp.), small sedges and several broad-leaved herbs; occurring sporadically are low, erect shrubs, tall herbaceous plants, and coarse horsetails (*Equisetum*), grasses and sedges. The chief mosses are *Aulacomnium palustre, Camptothecium nitens, Drepanocladus* spp. and *Sphagnum* spp. Prominent herbs include *Caltha palustris, Galium labradoricum, G. trifidum, Rubus acaulis, Carex disperma, Carex* spp., *Calamagrostis* spp., *Equisetum fluviatile,* and *Potentilla palustris.*

Though dominated by tamarack, this association is ecologically and floristically similar to the black spruce–peat moss association. " Like the latter, it develops on a peaty substratum, as a subclimax stage of a bog sere, and has a floor of peat-forming mosses. The main differences relate to the fact that the tamarack establishes in a *Drepanocladus-Carex-Betula* bog which continues in a relatively wet condition. *Sphagnum* mosses often invade this type of bog, developing there along with the tamarack. The extent of *Sphagnum* development is affected by the size of the bog, by periodic flooding, and by burning. With the growth of *Sphagnum* mounds, conditions become more favorable for black spruce and ericads but less suited to tamarack, sedges, and certain other plants of the tamarack vegetation " (Moss, 1953b). As Beeftink (1951) points out, tamarack is very intolerant of shade and can not succeed in competition with Labrador tea and other plants that soon cover the enlarging *Sphagnum* mounds, while black spruce flourishes under these conditions. Thus succession to the black spruce–peat moss association may take place. Following this, in turn, there may be a succession to the black spruce–feather moss association.

MOUNDED BOGS WITH ICE CORES. Brief reference may be made to a report (Moss, 1953b) of Alberta bogs with large mounds or ridges and alternating depressions, the elevated areas remaining frozen throughout the summer, while the depressions thaw out to the bog floor. Previous reports of mounded bogs with persisting ice cores (Palsa bogs) for the Boreal Region of North America are those of Wenner (1947) and Hustich (1939, 1950) in the forest-tundra region of Labrador. Hustich suggests that this type of bog may form the southern limit of the real permafrost region. The mounded bogs of northwestern Alberta are either within or close to the permafrost zone as depicted by Muller (1947). The conditions under which "Palsa" mounds are produced and maintained are discussed briefly by Moss in the light of Hanson's (1950) experience with solifluction and mound areas in Alaska.

This discovery of permafrost areas is of interest in connection with Hansen's discussion of bog origin and persistence in central Alberta. Though Hansen (1952) encountered no permafrost in these bogs, he believes that permafrost was actually necessary for their development, at least those formed on flat terrain. It is suggested that growth of *Sphagnum* was made possible in a semi-arid region by a high watertable held up by permafrost. Hansen further suggests that "amelioration of the climate to a degree that would eliminate the permafrost also would possibly result in the extinction of many muskegs formed on flat terrain".

Balsam Fir Vegetation

Halliday and Brown (1943) show balsam fir (*Abies balsamea*) as extending westward as far as north-central Alberta, where it is said to be of only light population intensity and restricted to moist forest habitats. It is most commonly found in mixed stands, with white spruce and poplar, in river valleys and round some of the lakes (Halliday, 1937). Confusion prevails as to the identity of the fir west of the Athabasca River, in central Alberta, for example, at Lesser Slave Lake. Halliday and Brown show the alpine fir (*A. lasiocarpa*) as extending northeastward into this region. The need of a critical study of the ranges of these fir species in Alberta and of the question of intergrading between them has been pointed out (Moss, 1953a). A recent study reported by Moss indicates that the fir at Battle Lake, some 50 miles southwest of Edmonton,

may be assigned to *Abies lasiocarpa,* though some of the trees approach *A. balsamea* rather closely. The balsam fir at Lesser Slave Lake is said (Moss, 1953) to occur generally in mixed stands with white spruce, aspen, balsam poplar and white birch, only locally in pure stands. Accompanying species are those commonly found in the white spruce and poplar associations of the region. An interesting associated species is the devil's-club (*Oplopanax horridus*). The ecological relationships of balsam fir in our region await critical study.

Pine Vegetation

One of the characteristic trees of the Boreal Forest, especially on sandy sites, is the jack pine (*Pinus banksiana*). This species extends westward, in northern Alberta, approximately to the line (Fig. 1) separating the Boreal and Boreal-Cordilleran regions. Associated with jack pine, in western Alberta, is lodgepole pine (*P. contorta* var. *latifolia*), a leading tree of the Rocky Mountains that has extended considerably farther east than most other Cordilleran species. The eastern boundary of lodgepole pine in northern Alberta is approximately the line between the Boreal and Boreal-Cordilleran, but in central Alberta this boundary lies much farther east to include areas near Lesser Slave Lake and close to Edmonton. Thus in the region between Edmonton and the Peace River, the ranges of these two pine species overlap. This situation, set forth clearly by Halliday and Brown (1943), has been further studied by Moss (1949, 1953a) who proposes minor changes in the boundary lines and presents evidence that many of the pines in the transition and overlapping regions are hybrids. It should be noted, too, that outliers of lodgepole pine occur still farther to the east, notably on the Caribou Mountains and the Cypress Hills. The intrusion of the lodgepole pine into the Boreal Region, the overlapping of ranges of the two pine species and the occurrence of intergrading pines serve to complicate efforts to classify the vegetation, whether in terms of phytogeographic zones or plant communities. These complexities suggest numerous intriguing and as yet unsolved botanical problems.

An effort has been made by Moss (1953a) to classify and characterize the pine vegetation of northwestern Alberta and to correlate this study with the pioneer work of Dowding (1929)

on jack pine in central Alberta and with the description by Raup (1946) of pine vegetation in the Wood Buffalo Park and near Lake Athabasca. The pine vegetation of these areas described by Raup differs significantly from pine communities elsewhere in Alberta, so far as reports indicate. Raup describes the jack pine vegetation of his region in two phases—that on sandy plains or ridges, and that on rocky hills. The former phase is somewhat like jack pine farther south but differs in several important respects, principally in its primary species, *Picea mariana, Cladonia rangiferina* and *Cetraria nivalis.*

Pinus banksiana–P. contorta ASSOCIATION. The pine vegetation in the greater part of our Boreal Region is probably best treated as one community and given the status of an association (Moss, 1953a). Within this association, two consociations may be recognized, the jack pine and lodgepole consociations, on the basis of species dominance. For each of the consociations a number of faciations may be distinguished by their ground cover. Two of these faciations are quite prevalent and rather well defined; (*a*) *pine–feather moss faciation,* on the more moist and more shaded sites, characterized by *Hylocomium splendens* and *Calliergonella schreberi,* along with various higher plants such as *Linnaea, Pyrola* spp., and *Cornus canadensis;* (*b*) *pine-heath faciation,* on the drier and more open parts of stands, characterized by *Arctostaphylos uva-ursi, Vaccinium vitis-idaea, Elymus innovatus, Oryzopsis pungens, Polytrichum* spp. and *Cladonia* spp. Common to both faciations are several species, including *Alnus crispa, Rosa* spp., *Salix* spp. and *Maianthemum canadense.*

ECOLOGICAL RELATIONSHIPS. "As is well known, jack and lodgepole pines are fire trees, commonly reproducing by seed following burning of stands. Since they are also light-demanding, they succeed on burned areas because their early growth is much faster than that of any spruce that may have started. Moreover, they send their taplike roots deep into sand and gravelly soils, making for success on apparently dry sites" (Moss, 1953a). The drier pine areas, such as tops and south-facing slopes of sand ridges, are generally occupied by the pine-heath faciation or by a treeless vegetation that may be called a "pine-heath associes". This has a large proportion of *Polytrichum piliferum, Cladonia* spp., small

grasses and sedges, as well as numerous broadleaved xerophytes. Produced by severe burning, this associes, through pine regeneration, may develop into the pine association. However, since both drought and burning militate against the success of the pine on these drier areas, the pine-heath associes tends to persist indefinitely as an edaphic climax. On more moist pine sites, where the pine-feather moss faciation tends to become climax, pine regeneration is generally good after burning and the pine community is restored. However, with prolonged absence of burning, succession to white spruce may occur.

The " pine-moss association " described by Dowding (1929) for xeric jack pine sites on sandhills of central Alberta is similar to the pine-heath associes. Dowding's " pine-heath association " of mesic sandhill sites resembles the pine-heath faciation. Where sandhill bases and bog margins merge, the vegetation consists of a highly variable mixture of pine and bog communities. Though Dowding describes this as a " pine-birch association ", it is perhaps best treated simply as transition vegetation.

CORDILLERAN FORESTS

Boreal-Cordilleran Transition

The broad transition zone which we have designated the Boreal-Cordilleran Region presents difficulties to the reviewer, partly because of the inherent complexity of the vegetation and partly because this vegetation has received relatively little critical study. The poplar vegetation of southwestern Alberta has already been discussed; that of the more northern foothills and mountain areas relates to pine and spruce vegetation presently to be considered. As already noted, white spruce extends through the Boreal-Cordilleran into the Subalpine and Montane regions, where it grows at the lower elevations, merging there with Engelmann spruce. Black spruce occurs not only in the bogs but to some extent on foothill and mountain slopes as far south as the Nordegg region. The role of black spruce will be discussed in connection with our presentation of spruce and lodgepole pine forests. Douglas fir and limber pine are of some significance, especially in the Montane Forest. Lodgepole pine, already noted as prominent in the western part of the Boreal, is the chief pioneering and dominant subclimax species in the Boreal-Cordilleran and Cordilleran regions. Alpine

fir becomes increasingly prevalent westward in the foothill-mountain transition region. This species and Engelmann spruce dominate in the climax association of the Subalpine Region.

In the following summary of available information on the chief types of forest vegetation in the Boreal-Cordilleran and Cordilleran regions, the reviewer leans heavily upon a recent unpublished report by Horton (1954). Permission to quote from Horton's excellent report is acknowledged below.

White Spruce Vegetation

On account of the gradual transition from white spruce to Engelmann spruce in the foothills and mountains, it is difficult, if not impossible, to draw a sharp boundary line between them. Moreover, certain of the published reports make no attempt to distinguish between the two species. This is unfortunate because the altitudinal occurrence of these trees indicates considerable difference in ecological amplitude. White spruce is reported by Halliday (1937) as one of the chief species of the Foothills Section between 3,000 and 5,000 feet elevations. Clarke and Cowan (1945), in amplifying their statement that white spruce and Engelmann spruce may be taken to separate the Boreal and Subalpine forests, outline the western limits of the former species in the region of Banff National Park. White spruce is said to extend in tongues up the main valleys, for example, up the Spray River to the upper falls, up the Bow to about Eldon, and up the North Saskatchewan to the forks. West of these points the valleys are occupied by Engelmann spruce. Eastward the valleys and lower slopes and also dry slopes at higher elevations have white spruce, when they have any spruce at all. Moist sites at higher elevations have Engelmann spruce and there is a considerable area of hybridization. An earlier report for the Banff region by Lewis (1923) states that the Engelmann spruce zone does not descend much below 6,800 feet and rises in places to nearly 8,000 feet. Lewis (1917) says that white spruce near Banff occupies marshy flats in the Bow valley and covers rocky slopes between 4,500 and 7,000 feet. Horton (1954) reports that Engelmann spruce (or an intermediate form) is the characteristic spruce in the Cordilleran forests, and typical white spruce in the foothills (Boreal-Cordilleran) region.

For an area in the mountains of southwestern Alberta, Cormack (1949) says that white spruce is the chief tree, though Engelmann spruce has been reported for the region. In discussing forest cover for the general "East Slope" region of Alberta, Cormack (1953) states that "White spruce is regarded as the climax tree species for this region, where it extends from almost timberline downwards for about three thousand feet". This statement, it must be pointed out, conflicts with the generally accepted opinion (as summarized in the preceding paragraph) that Engelmann spruce is the climax spruce species in timberline forest and in a broad zone well below timberline.

Apparently a white spruce association for the Boreal-Cordilleran region has not been recognized as such; yet data provided by Cormack (1949, 1953) and Horton (1954) seem to warrant this classification. Assuming the spruce vegetation described by Cormack for the lower slopes and the valleys to be dominated by white spruce (the upper slopes most likely by Engelmann spruce), and bringing to bear Horton's account and the reviewer's personal knowledge of the region, it becomes possible to make a rough synthesis in terms of a vegetational type or association. Cormack (1949) has provided an excellent general description of the virgin spruce forest along the Carbondale River and also a lengthy list of the species, with an indication of their relative abundance. While the proposed *Picea glauca* association occurs in several phases or faciations, the most prevalent climax phase is envisaged as follows: a dense stand of spruce, 100 to 130 feet tall and 15 to 30 inches d.b.h., and associated smaller trees of alpine fir; small tree and shrub strata, highly variable in nature, including *Salix* spp., *Cornus stolonifera, Lonicera involucrata, Viburnum edule* and *Vaccinium* spp.; herb strata, rather rich in species but quite variable and generally sparse, characterized by *Linnaea borealis* var *americana, Cornus canadensis, Equisetum arvensis, E. scirpoides, Mitella nuda, Petasites palmatus, Pyrola* spp., *Thalictrum* spp., *Carex* spp., *Habenaria* spp., *Osmorhiza obtusa, Smilacina* spp., *Actaea rubra* and *Lycopodium annotinum;* a rich deep floor carpet of "feather" mosses, especially *Hylocomium splendens, Ptilium crista-castrensis* and *Calliergonella schreberi,* with scattered lichens, mostly *Peltigera aphthosa.*

It will be noted that this association differs significantly from

the *Picea glauca* association of central and northern Alberta in having alpine fir as a leading constituent. However, the fir appears to be absent from certain situations, especially some of the river valley flats. Other phases of the present association are quite divergent in respect to the lesser flora, notably a phase that seems to be peculiar to the Montane Region, and well shown in the Carbondale area described by Cormack. Characteristic of this phase are *Rubus parviflorus, Clintonia uniflora, Disporum oreganum* and *Elymus glaucus,* also a rather rich fern flora. A second important variation of this white spruce association occurs chiefly in moist valley sites of the foothills, northward in our region, and is characterized by a strong black spruce element. Successional phenomena involving white spruce of the mountains will be dealt with later in this review.

Lodgepole Pine Vegetation

Lodgepole pine has been aptly described by Clarke and Cowan (1945) as a "temporary fire type running through all forest divisions and not diagnostic of any". Horton (1954) emphasizes the complicated picture presented by the lodgepole pine vegetation of the foothills and mountains. There are certain obvious correlations between the lesser flora and site, as also between this flora and pine stocking. Under open and/or dry conditions, prevailing species with the pine include *Arctostaphylos uva-ursi, Juniperus* spp., *Zygadenus elegans, Hedysarum* spp., *Antennaria* spp. and *Cladonia* spp. Open stocking in all but the extreme sites generally produces a luxuriant growth of grasses, especially *Elymus innovatus* and *Calamagrostis* spp., and such herbs as *Fragaria glauca.* In mesic well-stocked stands the "feather" mosses generally predominate, with a variety of shrubs and herbs, for the most part *Ledum groenlandicum, Vaccinium membranaceum, V. scoparium, Lonicera involucrata, Viburnum edule, Cornus canadensis, Petasites palmatus* and *Equisetum* spp.

Horton discusses the possibility of recognizing a lodgepole pine association under the name: *Pinus-Picea-Vaccinium–Elymus–Linnaea–Feather moss–Peltigera.* However, considering the wide variations related to density of pine stands, as well as the many regional and local habitat variations, also considering the dynamic nature of succession, he prefers to adopt the "continuum" concept

as expressed by Brown and Curtis (1952). Accordingly the general subclimax pattern, presented by our lodgepole pine forests, is looked upon by Horton as a vegetational "continuum". This is conceived of as "a continually varying series of species sorting along an environmental gradient mainly controlled by the vegetation itself". Horton says the most important interaction relates to succession which is dependent primarily on fire.

Lodgepole Pine to Spruce-Fir Climax

Succession from lodgepole pine to a spruce-fir climax vegetation has long been recognized by ecologists as a highly significant development in the Rocky Mountains. Recent discussions on the subject by Bloomberg (1950), Cormack (1953) and Horton (1954) have served to focus attention on certain vital issues, both theoretical and practical. The first two of these writers do not distinguish between white spruce and Engelmann spruce in their presentation. Horton differentiates between succession in the High Foothills, where white spruce-alpine fir is the climax, and succession in the Subalpine Region, where Engelmann spruce-alpine fir is climactic. He also discusses the trends for xeric, mesic and moist sites. However, Horton believes that the two spruce species are similar in their successional characteristics. These investigators are in general agreement that lodgepole pine expands to subclimax dominance through the frequency of burning and that succession to a spruce-fir forest takes place. But they are at variance in respect to certain important details concerning succession itself and also the stability and permanency of the spruce-fir association. The latter question is an integral part of the larger subject and will be included in the following discussion.

EARLY STAGES IN SUCCESSION. Cormack (1953) recognizes two general successional trends, each originating in a recent burn: (*a*) pine and spruce to climax; (*b*) pine to climax. In *a*, spruce and occasionally fir start off at approximately the same time as pine; in *b*, the earlier stages are characterized by either open or dense stands of pine, with spruce entering later. Of four stages recognized for trend *a*, the first two are designated *Ceratodon-Parmelia-Epilobium* and *Hypnum-Peltigera-Linnaea*, these stages being named after the most characteristic species of the ground vegetation. Corresponding stages of trend *b* are *Ceratodon-Parmelia*

and *Hypnum-Cladonia-Vaccinium.* Associated with *Ceratodon* and *Parmelia* spp., in the early stages, are said to be *Cladonia* spp. and hair-cap mosses as well as various herbaceous flowering plants. Incidentally the report of species of *Parmelia* as characteristic crustose lichens, in a hard ground cover for our region, comes as a surprise to the reviewer. Cormack admits that his proposed scheme is an arbitrary one. That it may be so regarded is supported by Horton's (1954) extensive investigation. The wide variations in ground flora of young pine stands, depending on density of stand and the nature of the site (reported above), as well as on various effects of repeated fires and burning intensity, present an exceedingly complex picture.

VARIATIONS IN LATER STAGES. For both "trends" recognized by Cormack, the last two successional stages are the same, viz., *Hypnum-Peltigera* and *Mnium-Clintonia-Menziesia,* the latter denoting the characteristic ground vegetation of the climax forest. Cormack lists numerous herbs and shrubs that comprise the relatively rich flora of this Forest. Horton states that Cormack's findings, though attributed to the whole "east slope" or Saskatchewan River drainage, apply, according to his observations, only to the Montane and the southern portion of the Subalpine region.

Significant aspects of succession reported by Horton may be noted here. The spruce species and alpine fir depend on topographical refugia from fire for their seed source. Such residual patches are common in the rough terrain of the region. There are relatively few pine stands without some degree of spruce understory. In the vicinity of a seed supply, the spruce may form a continuous layer along with alpine fir. Distribution and abundance of spruce in pine stands depend on proximity of a seed source, and on favorable site and competition (pine density). In general, most spruce become established under pine over an age range of 10 to 40 years following fire. Thus in old stands the spruce is predominantly even-aged or practically so. Spruce is initially slow-growing, but dominants reach the pine canopy between 70 and 160 years, generally in about 125 years. "From that time spruce waxes and pine wanes". Lodgepole pine has a maximum lifespan of 250–300 years. Dominant spruce trees usually live to well over 300 years. The maximum age found by Horton was

450 years. The rate of succession depends on the abundance and developmental rate of the tolerant species. Pine appears to prevail longer under such adverse conditions as dry sites and heavy stocking. Light ground fires and other conditions which permit pine reproduction in an old stand tend also to lengthen the sere. The duration of the sere seems to vary from 225 to 375 years. Black spruce is of some importance on lower slopes, northward from the Nordegg district. From bog refugia it extends into upland pine stands. It becomes established over a variable initial age range and may continue to reproduce thereafter by layerings. Usually it remains suppressed during its life-span which seldom exceeds 200 years. Aspen competes favorably with conifers only in localized protected sites of the mountains and higher foothills. In the lower foothills it is more successful, but even there it may be succeeded by pine in one generation. However, it is favored by burning because of its ability to propagate by suckering.

NATURE OF THE SPRUCE-FIR CLIMAX. For mountain slope forests near Blairmore, Bloomberg (1950) reports that lodgepole pine regenerated thickly on burns, stagnated at 150 years and was gradually succeeded by spruce to produce spruce-fir stands of great age and apparent stability. Remarkable, however, is the absence of any preparation on the part of apparently climax stands to perpetuate themselves, for spruce regeneration is said to be "conspicuous by its scarcity" and fir regeneration hardly profuse enough to fill in sparse gaps. Bloomberg furnishes evidence that the age-class distribution in these stands is directly attributable to fire and that without periodic burning the climax type tends to become decadent. He says fire is not only associated with the succession cycle leading to the establishment of the spruce-fir complex "but is actually the kingpin of the whole structure"; and "without fire in such proportions as to be catastrophic from a protection point of view there would be no valuable forests to protect". Cormack (1953) emphasizes the stability of the climax spruce-fir forest and gives an account of regeneration differing from that suggested by Bloomberg. He states that "reproduction and subsequent growth of spruce and fir occurs under openings in the forest canopy due to the windthrow of overmature trees" and that "large numbers of spruce and fir seedlings may be found growing on almost every moss-covered windfall".

Horton (1954) states that there is great variation in spruce and fir content in different climax stands and prefers to conceive of the climax as "a variable pattern". Different aspects of this variable spruce-fir climax are discussed. Horton found several stands where alpine fir was increasing rapidly and spruce on the wane. Despite its short life-span of about 200 years, fir has certain advantages over spruce, viz., its greater tolerance and its capacity to reproduce prolifically by both seed and layering. For these reasons alpine fir may be regarded as the culminating species. On the other hand, fir is greatly retarded by various factors, especially browsing by large game animals. Horton inclines to the view that where fir is kept down through browsing or other agencies, spruce will predominate. He says that spruce does continue to reproduce, though sparingly, in openings of the climax stand. Incidentally he agrees with various other investigators that spruce seedlings rarely become established in the dense moss mat of the forest floor, but often on rotten, fallen, fire-killed timber. Though Horton reaches no definite conclusion as to the permanency of the spruce-fir climax forest, he seems to agree with Bloomberg that this is actually an academic question. While alpine fir may well be regarded as a theoretical climax, fire is so frequent in the region that a forest is not likely to survive long enough for the fir to gain general dominance over spruce, a period of somewhat over 500 years being envisaged.

Picea engelmanni–Abies lasiocarpa Association

A comprehensive description of this association in Alberta has yet to be published. Nevertheless, data supplied by Cormack (1949, 1953) and by Horton (1954), as well as the reviewer's personal knowledge, make possible a brief account of its salient features. Actually the more important aspects, those pertaining to dominant species, general development and equilibrium, have been discussed above. It remains to indicate the internal structure and floristic composition of the association. For the following brief and rather tentative description, the present writer must assume the major responsibility.

Under the forest canopy formed by the two dominant trees, *Picea engelmanni* and *Abies lasiocarpa,* a few small tree species and large shrubs occur more or less sporadically. These include

Salix spp., *Alnus* spp. and *Sorbus scopulina*. Smaller shrubs are generally more prevalent—*Vaccinium membranaceum, V. caespitosum, Viburnum edule, Ribes lacustre, Rosa* spp., *Lonicera* spp., *Spiraea lucida, Rhododendron albiflorum*. Woody species restricted to the more southern parts of the region are *Acer douglasii* and *Ribes viscosissimum*. Certain of those common in the south (Montane Region) also extend northward but do not reach the more northern parts of our forest, e.g., *Menziesia glabella* and *Vaccinium scopulorum*. Still others are found mainly northward, e.g., *Vaccinium vitis-idaea* and *Empetrum nigrum*. On the basis of minor woody species alone, two or more faciations of the association are indicated. Herb strata, for the association as a whole, include species of *Equisetum, Carex, Juncus, Luzula, Habenaria, Smilacina, Saxifraga, Thalictrum, Viola, Ranunculus, Mitella, Pyrola, Osmorhiza, Epilobium, Fragaria, Castilleja, Linnaea borealis* var. *americana, Cornus canadensis, Parnassia fimbriata, Trollius albicaulis, Galium triflorum, Pedicularis bracteosa, Erigeron salsuginosus, Arnica cordifolia, Streptopus amplexifolius, Zygadenus elegans, Lycopodium annotinum* and various ferns and grasses. Important additions for the south of Alberta are *Clintonia uniflora, Xerophyllum tenax* and *Elymus glaucus*. Species that seem to appear only northward in the association include *Rubus pubescens* and *R. pedatus*. There is a rich ground cover composed chiefly of " feather " mosses, including the three species listed for most other coniferous woods in Alberta and species of *Rhytidiadelphus*, also species of *Mnium* and many others. Liverworts and lichens are prevalent in the moss carpet, especially the large lichen, *Peltigera aphthosa*. Mosses and lichens also cover windfalls and lower trunks of trees. It may be added that the *Picea engelmanni–Abies lasiocarpa* association of Alberta appears to be richer in species and less homogeneous than is the corresponding association, described recently by Oosting and Reed (1952), in the Medicine Bow Mountains in Wyoming. As these authors suggest, further studies of this wide-spread subalpine community should be made.

Other Coniferous Associations

The Montane Forest, as it occurs in Alberta, is generally said to be characterized by Douglas fir, lodgepole pine, Engelmann spruce and white spruce, with some limber pine on the foothills

and clumps of aspen at the contact with the Grassland Formation (Halliday, 1937; Moss, 1947; Horton, 1954). The very rare occurrence here of western white pine (Moss, 1944) and of ponderosa pine and western cedar (Cormack, 1949) is of considerable interest. However, as Horton points out, the Montane Forest in Alberta is recognized better by its shrub and herb species than by its tree dominants. Species peculiar to the forest are said to be *Rubus parviflorus, Ribes viscosissimum, Berberis repens,* and *Clintonia uniflora.* This Forest occurs at elevations of 4,500 to 6,500 feet in the Waterton district and extends northward to the Crowsnest Pass. Douglas fir and various of the associated species have apparently intruded from British Columbia along passes through the Rocky Mountains. Isolated stands or patches of Douglas fir occur in the Porcupine Hills, in the Bow Valley and at Jasper. Brief accounts of vegetational units dominated by Douglas fir and by limber pine have been given by Moss (1944) for rocky ridges in the park belt region lying between Waterton Lakes Park and Crowsnest Pass.

DOUGLAS FIR VEGETATION. Small stands of this tree (*Pseudotsuga taxifolia*) are said to occur locally on sandy-gravelly foothill slopes and on the better protected slopes of rocky ridges. The tops and exposed slopes of these ridges, which are subjected to strong desiccating winds, are characterized by limber pine. An interesting array of plants appears in these Douglas fir stands. A few of the species listed by Moss are: *Rubus parviflorus, Rosa* spp., *Amelanchier alnifolia, Acer douglasii, Clematis columbiana, Spiraea lucida, Lonicera glaucescens, Agropyron trachycaulum, Calamagrostis* spp., *Aster conspicuus, Erigeron speciosus, Heracleum lanatum, Glycosma occidentalis, Smilacina racemosa, Disporum trachycarpum, Hieracium griseum, Erythronium grandiflorum, Cystopteris fragilis* and *Claytonia lanceolata.*

LIMBER PINE VEGETATION. Exposed to very strong winds on the dry slopes and summits of rock ridges, the limber pine (*Pinus flexilis*) trees are generally dwarfed and distorted. Actually the pine forms an open community with many exposed areas of various sizes. Only locally do the trees provide shade and otherwise influence accompanying species. In most places the rock has weathered to form a thin loose shaly soil; elsewhere it is practically

unweathered. In spring and early summer these areas are veritable rock gardens, displaying a wealth of form and color. Of the numerous species listed by Moss for various aspects of these "pine ridges", the following are recorded here to indicate the range in life-form and flora: *Arctostaphylos uva-ursi, Juniperus horizontalis, J. sibirica, Populus tremuloides, Potentilla fruticosa, Shepherdia canadensis, Phlox alyssifolia, Physaria didymocarpa, Sedum stenopetalum, Astragalus pauciflorus, Aster conspicuus, Penstemon confertus, P. nitidus, P. eriantherus, Arabis* spp., *Draba* spp., *Townsendia parryi, Phacelia sericea, P. linearis, Polemonium pulcherrimum, Selaginella densa, Agropyron spicatum, Artemisia* spp., *Cryptantha bradburiana, Erigeron* spp., *Antennaria* spp., *Allium cernuum, Solidago* spp., *Paronychia sessiliflora, Lychnis drummondii, Hedysarum sulphurescens, Lupinus leucopsis.*

ALPINE VEGETATION

Few papers have been published on the alpine vegetation of Alberta, and these are quite limited in their scope and treatment. More has been written about similar vegetation lying to the south in the United States and that of the far northern mountains beyond Alberta (Raup, 1934, 1947a; Porsild, 1945). By interpolation one can arrive at a fairly good general understanding of our own region. A summary account of ecological aspects of Rocky Mountain alpine vegetation has already appeared (Daubenmire, 1943). Therefore the present review aims merely to sketch the salient features of our region and to correlate some of the reports that have appeared. Discussion of arctic-alpine problems, including Hultén's contribution to the phytogeography of the region, is largely excluded from this article. For comprehensive reviews of these subjects reference may be made to Raup (1941, 1947b).

Alpine vegetation occurs between timber line of the subalpine forest and snowline. For Alberta mountains as a whole, timber line varies from an altitude of 6,500 to 8,000 feet, the line being, in general, progressively higher southward. Daubenmire (1943) points out that nowhere is the youthfulness of Rocky Mountain topography more important vegetationally than in the alpine zone. "Here the surface is essentially an alternation of rocky outcrops with depressions of varying degree of imperfect drainage, and the soil, when present, varies from peat to gravels which are practically

devoid of organic matter". The plants are said in relation to this striking edaphic heterogeneity to form communities seldom extensive or very homogeneous. As Daubenmire also reports, alpine vegetation consists almost entirely of perennials, mostly of the caespitose habit and either herbaceous or suffrutescent. The Rocky Mountain alpine flora has long been known to contain many arctic species. Gray and Hooker (1880) stated that it is an arctic flora, or rather prolongations of it southward along the mountains, with certain admixtures of species from more southerly regions. Lewis (1923) notes that many of these arctic species in our region have a circumpolar distribution, e.g., *Dryas octopetala, Silene acaulis, Sedum rhodiola, Saxifraga cernua, Oxyria digyna, Polygonum viviparum* and *Arctostaphylos alpina.* Rydberg (1914) deals with this subject for the Rocky Mountain region as a whole, and Daubenmire (1943) gives a concise summary. Briefly it may be said that our alpine flora derives from two main sources—the arctic tundra and local endemic areas. According to Rydberg, more than one-third of the alpine species of the Rockies are endemic, though several of them are apparently derived from glacial or arctic plants.

Vegetational Zonation

The alpine vegetational formation is often divided into three zones, these being delimited, respectively, by forest (timber) line, tree line and scrub line (Lewis, 1923). Forest line is the altitudinal limit of forest grown trees. The transition from subalpine, spruce-fir, forest to tree line is usually very gradual and is characterized by groves of trees and isolated individuals, the latter often stunted and distorted; hence this zone is known as "krummholz". For the Banff region Lewis places this tension belt at about 7,200 feet. The chief tree species of this zone in our region are alpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), alpine larch (*Larix lyallii*) and white-bark pine (*Pinus albicaulis*). In the scrub zone these species become even more stunted, the main stem often creeping with short erect shoots and assuming fantastic forms. Trees of the "flag" shape grow here; also matted atoll-like rings of offspring are produced by layering. It is amongst the groves of these zones that the "alpine meadows" are found. "Of many different types according to aspect, slope of ground and amount of moisture, the vegetation here shows more diversity and

greater profusion of flowers than any other region either in the temperate or tropical belts" (Lewis, 1923). Beyond the scrub line, to the region of perpetual snow or ice, the vegetation consists of small plants, many having a circumpolar distrubution, as noted above.

Chief Communities

Alpine habitats, in their great diversity, support varied and heterogeneous assemblages of plants. The following summary of the more prevalent communities is largely adapted from Lewis (1917) on the Banff region and Daubenmire's (1943) general account.

BOULDER-FIELD VEGETATION. The boulders of old moraines and rock-slides are characterized by crustose lichens and a scant flora of crevice and creeping plants, such as *Oxyria digyna, Penstemon fruticosus, Dryas octopetala, Lychnis apetala, Sibbaldia procumbens, Poa alpina* and *Salix nivalis.*

FELL-FIELD VEGETATION. Gravel areas commonly support a sparse vegetation in which low rosette and mat-forming species predominate, e.g., *Dryas octopetala, Silene acaulis, Erigeron* spp., *Polemonium* spp., and certain grasses and sedges.

ALPINE MEADOW. Occupying the more mesic habitats, and characterized by a rich and diversified flora, this so-called "meadow" may be described in two phases; (*a*) mat-grassland, with a preponderance of grasses and many early-flowering broad-leaved plants, including species of *Poa, Agrostis, Festuca, Trisetum, Potentilla, Anemone, Heuchera, Sieversia, Pedicularis,* also, *Polygonum viviparum* and *Myosotis alpestris;* (*b*) mat-herbage, dominated by herbs, with scattered grasses, the growth being less luxuriant than in the mat-grassland, including *Dryas octopetala, Sibbaldia procumbens, Saxifraga* spp., *Potentilla* spp., *Poa alpina* and *Festuca ovina.* The following type is also prominent in "alpine meadow", as this is understood by some writers.

HEATH VEGETATION. Commonly found between the groves of conifers in the transition zone, this ericaceous vegetation is characterized by *Cassiope mertensiana, C. tetragona, Phyllodoce empetriformis, P. glanduliflora, Pedicularis bracteosa* and *Saxifraga* spp.

SNOW-PATCH FLORA. Where snow remains in moist protected areas until late summer, this characteristic flora appears, the more common species being *Erythronium grandiflorum* var. *parviflorum, Anemone occidentalis, Ranunculus eschscholtzii, Valeriana sitchensis, Antennaria racemosa, Carex scirpoidea.* Some of these plants, notably *Erythronium* (snow lily), can often be seen in flower at the edge of snow-banks in August.

ALPINE BOG. This highly variable type occurs in several phases, two of which are prevalent: (*a*) sedge bog, dominated by species of *Carex*; (*b*) willow bog, dominated by shrubby willows. Associated therewith are grasses and species of *Eleocharis, Ranunculus, Caltha* and *Trollius.* Mosses are often present and there is usually a considerable accumulation of sedge or moss peat.

Environmental Factors and Forest Line

The replacement of forest by forms of alpine vegetation is doubtless brought about by the interplay of many factors, involving topography, substratum, insolation, temperature, precipitation, wind velocity, snow, burning and biological agencies. As Daubenmire (1943) points out, there is a lack of sufficient research in the way of controlled experimentation to warrant very definite conclusions concerning the relative effects of different environmental factors. Yet, certain conclusions, drawn mainly from general field observations, are indicated.

Shaw (1909) emphasizes snow, rather than wind, as the principal cause of timber lines and alpine grassland. However, his study pertained more to the Selkirks than to the Rocky Mountains. Lewis (1923) believes that wind and snow are usually the two main factors tending to limit forest growth in alpine regions of the Alberta mountains. Griggs (1938) concludes that wind, not low temperature, puts a limit to upright tree growth in these mountains. Daubenmire (1943) states that the evidence from various sources points to the conclusion that " throughout most of the Rockies the upper altitudinal limits of tree species which reach timber line are determined primarily by high wind velocity and that wind is effective by promoting transpiration at times when the soil is frozen and plants cannot absorb or conduct moisture with sufficient rapidity to replace that lost by transpiration ".

The possibility of a general shift in the timber line level of our

region during recent times has been investigated by Griggs (1938). He had previously found the forest to be invading the tundra at Kodiak in Alaska. From studies done at various points, including Glacier National Park, Lake Louise and Jasper, Griggs concludes " that in the Rocky Mountains, timberline and therefore climate is static, or more precisely, that any change which climate may be undergoing is at a rate of a different magnitude than at Kodiak, too slow to be detected by the methods employed ". Most examples of forest advance in our region, Griggs was able to explain in terms of re-invasion of ground from which forests had been removed, mostly by fire. The general conclusion reached by Griggs regarding climate is of considerable interest in connection with the prevailing idea that the mountain glaciers of our region are receding.

Alpine Plant Succession

Xeroseres and hydroseres have been indicated for the Alberta alpine region but no critical work has been reported. Reference may be made to investigations, such as those of Whitfield (1933) and Cox (1933) in the United States, as representing the kind of study that should be done in our region. There is one paper dealing with plant succession in the Canadian Rockies that should be mentioned here. This is by Cooper (1916) on the Mount Robson region which lies close to the British Columbia–Alberta border. Though Cooper's study deals with forest zones, rather than the alpine, it is mainly concerned with primary seres and therefore relates closely to succession under alpine conditions. Cooper says two primitive surfaces are left bare by the retreat of the ice—rock surfaces and moraines. Each of these soon generates another, so that four habitats are offered to invasion by plants; rock surfaces and talus; moraines and shingle flats.

MARSH AND REED SWAMP VEGETATION

For our present purpose, the terminology used in a recent paper (Moss, 1953b) will be adopted. A marsh is defined as a grass-sedge-rush community, usually without mosses or much peat accumulation and the floor covered with water one or more months of the growing season. A shallow marsh, having water only a small part of the growing season, is a wet meadow. A reed swamp is a very wet marsh characterized by such plants as bulrushes

(*Scirpus*), cattails (*Typha*) and coarse grasses (e.g., *Scolochloa festucacea*). A bog is characterized by peat-forming mosses, commonly *Sphagnum*, also by ericads and conifers. Marsh-bog transition vegetation is not uncommon in our forested regions.

Fresh-Water Areas

Marsh and reed-swamp vegetation has been described for representative portions of forested Alberta apart from the Rocky Mountains. Concerning this vegetation in our prairie parkland region, little has been published; but a brief account for the corresponding part of Saskatchewan has appeared. Marshes and reed swamps are associated with the numerous ponds and lakes throughout much of Alberta. In general there is a gradual transition from aquatic vegetation through reed swamp to marsh on the margins of these bodies of water. Depressions without open water, and occupied by marsh, are also common. In the prairie region a marshy border of a shallow lake (slough) may be flanked by a narrow bank of willows but usually merges gradually with the prairie grassland. In the forested regions there is generally a succession of marsh to willow (sometimes with alder), followed by balsam poplar and white spruce. However, under certain conditions succession is from marsh to either *Hypnum* (*Drepanocladus*) or *Sphagnum* bog and to bog forest.

In their pioneer work on reed swamps and marshes ("low moors") of central Alberta, Lewis et al. (1928) show these to be of diverse types and complex relationships. Only a few features will be noted here. (Emended specific names are substituted for certain of those appearing in the paper). The chief dominant species of reed swamps are *Scirpus validus, Typha latifolia, Scolochloa festucacea* and *Carex atherodes*. Common associated plants are *Sagittaria cuneata, Sparganium* spp., *Equisetum fluviatile* and *Lemna minor*. Leading dominants of marshes are *Carex aquatilis, C. rostrata, C. diandra, C. lasiocarpa, Glyceria* spp., *Calamagrostis inexpansa* and *C. canadensis*. Accompanying plants include *Alopecurus aequalis, Poa palustris, Hordeum jubatum, Beckmannia syzigachne, Eriophorum* spp., *Eleocharis palustris, Scutellaria epilobiifolia, Galium trifidum, Ranunculus sceleratus, Sium suave, Cicuta* spp., *Stellaria* spp., *Aster* spp. and *Stachys palustris* var. *pilosa*. A common sequence on borders of alkaline

sloughs is reported somewhat as follows: Aquatics → *Typha–Scirpus* → *Scolochloa–Carex atherodes* → *Glyceria–Carex* spp. → *Salix* spp. → *Populus balsamifera.* Marshes extending across wet basins appear generally to be acid (pH about 6) and are characterized by *Carex diandra, C. lasiocarpa, C. rostrata, C. aquatilis, C. chordorrhiza, Poa palustris, Eriophorum* spp., *Triglochin maritima, Equisetum fluviatile, Potentilla palustris, Menyanthes trifoliata* and a mat of *Hypnum* (*Drepanocladus* spp.) on the floor.

A somewhat similar account of marshland is given by Raup (1935) for the Peace-Athabasca delta region in northeastern Alberta. The flood-plain and delta lands have extensive marshes, ranging from aquatic shore associations to grasslands. The sloughs and wet meadows are separated by natural levees and other alluvial deposits, tenanted by willow clumps or timber. Two of the most widespread species, *Calamagrostis canadensis* and *Carex trichocarpa* var. *aristata* (*C. atherodes*), form extensive "hay meadows" throughout the lowlands. Raup describes this rather complex vegetation in some detail, including common successional trends. The main hydrarch sequences may be summarized as follows: *Potamogeton* → *Nuphar–Sagittaria–Myriophyllum* mixtures → *Scirpus–Typha–Glyceria–Eleocharis* mixtures → *Carex rostrata* (or, *Carex atherodes* → *Calamagrostis*) → *Salix planifolia* → *Salix–Alnus–Populus* mixtures → *Picea glauca.*

Meadows, wet marshes and related vegetation of the Peace River region in northwestern Alberta are described by Moss (1953b). Readers are referred to this recent paper for a list of aquatic and shore-line species and a brief account of reed swamps, marshes and wet meadows, including retrogression of marsh through burning and succession of marsh types to bog.

Only brief notes have been published on marsh vegetation in the prairie region of southeastern Alberta. Slough borders there are characterized by *Scirpus validus, S. americanus, S. paludosus, Typha latifolia, Hordeum jubatum, Beckmannia syzigachne, Alopecurus aequalis, Eleocharis palustris, E. acicularis, Carex lanuginosa, C. praegracilis, Puccinellia nuttalliana, Deschampsia caespitosa, Agrostis scabra, Iva axillaris* and species of *Juncus, Rumex, Atriplex, Chenopodium* and *Polygonum.* Less stagnant marshes found in sluggish water courses and stream flats have

extensive stands of *Polygonum coccineum* and *P. amphibium* var. *stipulaceum*. The more saline depressions often support an abundance of *Puccinellia nuttalliana, Distichlis stricta, Spartina gracilis, Salicornia rubra, Suaeda depressa, Glaux maritima, Iva axillaris, Atriplex nuttallii* and *Monolepis nuttalliana*. In the extreme south of the Province, some of the drier lowlands, such as flats of river valleys and coulee bottoms, are dominated locally by grasses (*Agropyron smithii, Distichlis stricta*), sagebrush (*Artemisia cana*) and greasewood (*Sarcobatus vermiculatus*).

Saline Marshes and Meadows

Of considerable interest is the account by Rawson and Moore (1944) of rooted aquatic plants and lake shore species in the prairie parkland of Saskatchewan. It may safely be assumed that the lakes of the eastern prairie-parkland region of Alberta are quite similar to those described for Saskatchewan. According to Rawson and Moore, most of the lakes are shallow, with no outflow and with a high degree of salinity. The majority have from 300 to 30,000 p.p.m. of total solids. The salts are chiefly sulphates of magnesium or sodium. The pH of these lakes (mostly 7.8 to 8.9) indicates a moderately alkaline condition, " not sufficiently important to justify their local description as alkaline, rather than saline, lakes ". The more common rooted aquatic plants are reported in relation to their occurrence in lakes of varying salinities. The fennel-leaved pondweed (*Potamogeton pectinatus*) is the most widespread, ranging from fresh water to a lake with a salinity of 20,000 p.p.m. Ditchgrass (*Ruppia*) is also highly resistant to salinity. *Chara* is reported for a lake with a salinity of 7,870 p.p.m. and in all of the lakes of lesser salt content. Other species for which salinity range is shown include: *Potamogeton richardsonii, Myriophyllum spicatum, Utricularia macrorhiza, Hippuris vulgaris, Sagittaria cuneata, Potamogeton vaginatus* and *P. zosteriformis*. Plants common at or near the water's edge of these lakes include *Scirpus paludosus, Typha latifolia* and *Carex* spp. The exposed shores of the saline lakes are said to have a characteristic flora of halophytes. Those found in the more saline locations are *Salicornia rubra, Distichlis stricta, Suaeda erecta, Atriplex hastata* and *Triglochin maritima*, tending to occur in this order, progressively from the lake to less saline soils.

For parts of the Salt Plain region south and west of Fort Smith, in the northeast corner of Alberta, Raup (1935) has described a distinctly halophytic flora. The most characteristic feature of these Plains is said to be the salt marsh vegetation which grows in undrained depressions. Leading species are *Salicornia europaea, Puccinellia nuttalliana, Suaeda depressa, Spergularia salina, Plantago eriopoda, Glaux maritima, Triglochin maritima, Chenopodium rubrum, Distichlis stricta* and *Hordeum jubatum.* Somewhat similar vegetation has been described by Moss (1953b) for small saline meadows near Fort Vermilion, well northward in Alberta.

MISCELLANEOUS TYPES OF VEGETATION

Badland Areas

Extensive badlands occur along the Red Deer river, especially near Drumheller and Steveville. These are famous as a source of dinosaur skeletons. Other smaller badlands are found elsewhere in southeastern Alberta. The eroded faces and banks of these areas are almost devoid of vegetation but have patches of prairie and other plants on the more favorable sites. Among the more conspicuous species are the sage-brushes (*Artemisia longifolia, A. cana*), creeping juniper (*Juniperus horizontalis*) and bearberry (*Arctostaphylos uva-ursi*). On flats between the badland hillocks, cacti (*Opuntia polyacantha, O. fragilis*) are prevalent.

Prairie Sandhills

Contrasting sharply with the pine sandhills and ridges of central and northern Alberta are the low sandhills of the mixed prairie region, such as those lying southwest of the Cypress Hills near Lake Pakowki. These hills are in part stabilized by vegetational cover composed chiefly of the prairie grasses. Other parts are subject to active dune formation and are characterized by *Sporobolus cryptandrus, Oryzopsis hymenoides, Calamovilfa longifolia, Elymus canadensis, Cryptantha fendleri, Rumex venosus* and *Psoralea lanceolata.* Associated with these sand-loving species, certain shrubs are often found, notably *Prunus demissa, Rosa arkansana, Juniperus horizontalis, Symphoricarpos occidentalis* and *Elaeagnus argentea.* Locally willow clumps and even poplar trees are well established, presumably where the water table is fairly high. These include *Salix interior, S. bebbiana, S. amygdaloides,* aspen poplar and cottonwood (*Populus sargentii*).

Rivers and Creeks

The region provides a great diversity of stream courses, from rushing mountain creeks to the great rivers, the latter flowing through the forested areas or through the plains. Obviously many kinds of vegetation are supported by the waters, banks, flats, lagoons and deltas of these various streams. However, very little has been published on the subject for our region. The most comprehensive work is that of Raup (1935) for northern Alberta, especially his account of the vegetation of stream courses and river deposits in the Peace-Athabasca delta region. There is also a brief account of aquatic and marginal vegetation of creeks and rivers in the Peace River region by Moss (1953b). Poplar vegetation of river flats in the prairie parkland of southwestern Alberta has been described briefly by Moss (1944). The forested margins of the Carbondale River in the mountains of southwestern Alberta are described by Cormack (1949).

Raup's (1935) paper may be consulted for an account of some rather special topics pertaining to lagoon and delta conditions. Presented here is merely a general picture of the present writer's conception of the characteristic flora of creeks and rivers in the Boreal Region of Alberta. This is based partly on the published papers and partly on personal observations. The more sluggish waters have such submerged and emergent species as *Myriophyllum exalbescens, Sagittaria cuneata, Hippuris vulgaris, Sparganium multipedunculatum, Nuphar variegatum, Ranunculus trichophyllus, Polygonum amphibium* var. *stipulaceum, Lemna trisulca, Callitriche* spp. and *Potamogeton* spp., especially *P. richardsonii.* Stream banks and flats are characterized by *Scirpus rubrotinctus, Glyceria* spp., *Typha latifolia, Juncus alpinus, J. nodosus, Equisetum palustre, E. pratense* and *E. arvense,* also by such woody plants as *Salix interior, S. arbusculoides, S. lutea, S. planifolia, S. lasiandra, S. subcoerulea, Alnus rugosa, Cornus stolonifera, Populus balsamifera* and *Picea glauca.* Less prominent plants include: *Poa palustris, Carex rostrata, Cinna latifolia, Parnassia palustris* var. *neogaea, Achillea sibirica, Sium suave, Epilobium glandulosum* var. *adenocaulon, Erigeron philadelphicus, E. lonchophyllus* and *Stachys palustris* var. *pilosa.* Where balsam poplar and white spruce dominate near the water's edge, as they commonly do, the herbs and shrubs of these associations generally form a luxuriant

growth. Streams flowing through marsh or bog usually have various sedge species along their banks.

Flats of rivers in the prairie parkland of southwestern Alberta are commonly dominated by poplars and willows, with which are associated birch, alder and a variable assemblage of herbaceous species (Moss, 1944). The leading poplar species are *Populus angustifolia, P. acuminata, P. sargentii, P. trichocarpa* (near the Mountains) and *P. balsamifera.* There is said to be evidence of hybridization between certain of the cottonwoods and also between the two balsam poplars. The chief willows are *Salix lutea, S. caudata, S. interior* var. *pedicellata, S. melanopsis* and *S. amygdaloides.*

Virgin coniferous forest along the Carbondale River in the mountains of southwestern Alberta is well described by Cormack (1949) in his study of trout streamside cover. Spruce is the chief tree on the banks of the river and on the river flats. "On the immediate banks, often overhanging the water, willow and alders, together with a number of other small trees and shrubs, fill in the intervening spaces between the tall spruce". The most constant feature is the luxuriant, continuous moss carpet over soil, boulders and windfalls. Near the river margin the mossy, overhanging banks are tenanted by various shade-loving shrubs, ferns, horsetails, sedges and broad-leaved flowering plants. (See our review of spruce vegetation).

Calcareous Bogs

A small number of these unique bogs is known to occur in south central Alberta, near Edmonton. They are associated either with *Sphagnum* bogs in shallow depressions or with spruce-poplar woods on flats below a valley slope. Apparently lime-charged water from springs seeps in slowly to produce conditions suitable for an unusual kind of bog development and a characteristic flora. The surface of the bog consists of peaty mounds and shallow pools of water, the bottoms of the pools being whitish with marl deposit. The mounds, which are of various shapes and size, support a mixed vegetation, generally with mats and cushions of small mosses and scattered herbs, shrubs and small trees. Unfortunately the bryophytic flora has not been studied. Intermixed with the mosses, the little club-moss *Selaginella selaginoides* is often found.

Turner (1949) has listed the chief herbaceous and woody species for one of these bogs. Leading herbs are *Tofieldia glutinosa, Triglochin maritima, Allium schoenoprasum* var. *sibiricum, Carex viridula, Juncus longistylis, Dodecatheon pauciflorum, Lobelia kalmii, Gentiana macounii* (*G. tonsa*), *Pinguicula vulgaris* and *Antennaria pulcherrima.* Bog birch is usually present; also willows, including *Salix candida* and *S. glauca* var. *glabrescens.* Small trees of *Betula papyrifera, Larix laricina* and *Picea* spp. often become established on the larger hummocks.

Mountain Peat Bogs

Sphagnum bogs, though prevalent in our northern foothills, are apparently rather uncommon in the mountains. In any case they have not been described. Nor have other bog-like areas of the Alberta mountains received much attention. One rather common type, the "hangmoor", has been studied to some extent by foresters. Crossley (1951) gives a brief account of this interesting formation, with particular reference to the soil. He says hangmoor peats are found on gentle slopes where the ground water, being held up by the relatively impervious nature of the till, passes through them horizontally. The vegetational cover is said to be predominantly sedge, commonly with a fairly dense cover of dwarf birch, with some willow and a sparse stand of spruce. The hangmoor merits further study.

APPLIED ECOLOGY AND CONSERVATION

This review has thus far referred only briefly to certain practical problems relating to our vegetation, such as overgrazing of prairie grassland and regeneration of desirable timber stands. Even under the present heading there is no intention of dealing in any comprehensive way with the application of ecological principles to problems of utilization and conservation of vegetational resources. It is proposed only to draw attention to a few of the major issues pertaining to the utilization of our two main types of vegetation, prairie and forest, and to indicate how these issues are currently being regarded by administrators and by investigators.

Range Problems

It is perhaps fitting to refer first to the problem of providing suitable range for "the monarch of the plains", the bison (buffalo). The main bison herd, now located in Wood Buffalo Park, includes

not only the northern or wood bison but also a large element of the plains bison, the latter having been moved there several years ago from a Reserve in south-central Alberta. In his studies on range conditions in Wood Buffalo Park, Raup (1933, 1935b) emphasizes that sedge sloughs provide the main food supply for the bison, especially during the winter. He notes that the problem of winter feed seems to be the critical one for bison in the north. Soper (1941, 1951, 1952) has written a comprehensive account of the northern bison and has also reported on the flora and fauna, including the plains buffalo, as currently found in Elk Island Park, near Edmonton. Banfield's (1947) bulletin on the mammals of Waterton Lakes National Park includes a discussion of range conditions there. Several reports, some in mimeographed form, have been issued by Cowan (1952) and others on grazing and browsing conditions for wildlife in the Rocky Mountains.

Critical studies of our native pasture lands commenced in 1927 with the establishment of the Dominion Range Experiment Station, the first institution of its kind in Canada, near Manyberries in southeastern Alberta. Important work has been done on the botanical composition, carrying capacity and utilization of ranges and on the chemical composition of native forage plants (Clarke et al., 1930 to 1945). Research under the Federal Department of Agriculture is continuing in Alberta, that relating to the foothills ranching region being now directed from the Experimental Station, Lethbridge. University botanists, whose papers on prairie vegetation are reviewed above, have made significant contributions, as also has Hanson (1951, 1952, 1953) in his work with the Eastern Rockies Conservation Board. These various studies have helped to provide a scientific basis for advising ranchers regarding their ranges and for the framing of policy pertaining to the classification and utilization of areas.

Forest Problems

Until recently forestry officials in our region have devoted their attention almost exclusively to the administration of timber lands and to the most insistent of all forest problems, that of burning. Even so, forest fires have been rampant and have taken tremendous toll. However, it is hoped that, with improved facilities being provided, forest fires will be located more quickly and controlled

more effectively in the future. Until recently only a few ecological studies have been carried out by foresters in Alberta. Of these, studies on forest site indicators by Holman (1929), Parker's (1942) work on site criteria and Halliday's (1937) classification of forests may be mentioned.

Within the last few years the outlook has changed considerably. In 1949 the Alberta Government launched a survey of the Province's forest resources, with a view to the preparation of forest inventories and cover maps. Since 1951 the Canadian Government has been participating in this program which combines air photography and mapping with the study of sample areas by ground crews. Alberta foresters have also been showing an active interest in ecological research. Bloomberg (1950) reaches the conclusion that fire has a positive and causative effect on the establishment of spruce as a climax type, and poses the interesting question: "What will be the state of affairs when the ideal of complete fire protection is realized?". Assisted by the Alberta Department of Lands and Forests, Cormack (1949, 1953), University botanist, has carried out several studies of mountain vegetation in relation to stream flow, watershed protection, strip mining and forest succession. The Federal Government has greatly expanded its forest research facilities during recent years. In Alberta, ecological studies on different forest types have been initiated, for example, the study by Horton (1954) on the ecology of lodgepole pine (already reviewed at some length). Attention is being given to forest soils (Crossley, 1951) and to regeneration of desirable forests on denuded or poorly stocked areas (Crossley, 1952). The Federal Government has also established in Alberta a laboratory for research in forest biology, especially investigations of insects and diseases affecting forest trees; and good results are already coming from this centre. "The most notable post-war development in Alberta has been the establishment of the Eastern Rockies Conservation Board. This joint board, supported by the Federal and Provincial Governments, is charged with responsibility for protecting the eastern slopes of the Rocky Mountains, in which rise the headwaters of the Saskatchewan River and its tributaries"—quoted from "Canada's Forests, 1946–1950", Department of Resources and Development, Ottawa, 1952. This reference introduces the final section of the present review.

Watershed Problems

Particular reference is to be made here to Alberta's great watershed, the east slope of the Rocky Mountains. It should be noted, however, that watershed problems exist in many other parts of Alberta, and especially in agricultural areas. Attention is directed to an excellent bulletin by Toogood and Newton (1950) on water erosion in Alberta.

Concerning the watershed of the Saskatchewan River, commonly known as " The Eastern Slopes ", it has been authoritatively stated that " the dominant interest in this area, particularly from the federal standpoint may be said to be the regulating effect of forest cover on the flow of streams originating within the watershed " (Kennedy, 1948). The main responsibilities of the Board (to which reference has been made above) are briefly as follows: to provide projects and facilities required for the conservation of the forests and the protection of the watersheds in the area; to protect the forests of the area from fire, etc.; to conserve, develop, maintain the forests in the area with a view to obtaining the greatest possible flow of water in the Saskatchewan River and its tributaries.

During the past five years there has been much discussion on this important project. Complex natural phenomena are being investigated and attempts must also be made to resolve conflicting human interests. The main objective of watershed control may seem to conflict with one or more of several desirable uses of the region, such as: production of high-grade timber; bountiful supply of trout and big game; summer grazing for domesticated animals; aesthetic and recreational purposes. Of particular interest to ecologists is the stress the Board places on the " multiple-use " concept. The aim appears to be three-fold—to maintain the watershed in its original condition or better, to ensure optimum use of all resources in perpetuity, and to co-ordinate the various uses. One of the more contentious problems, that of grazing use of forest lands, has been discussed by Hanson (1952). He maintains that properly managed grazing fits nicely into a multiple-use land management where watershed value holds a place of prime importance.

In a comprehensive discussion of the Board's views on multiple forest use, Fellows (1952) emphasizes that water yield is the prime

concern and that the season at which water is available may be just as important as the total annual flow. Along with the growing demand for water, there is apprehension over the possibility of a diminishing supply. "The great glaciers of the Rockies, which contribute substantially to the summer flow of many of the larger streams, have been shrinking steadily for a number of years. In effect, this means that these streams are drawing on capital reserves of moisture rather than on the current snowfall and rainfall alone. Eventually this source of water may become almost negligible, and a compensating supply must be found elsewhere". Fellows goes on to discuss the effects of logging, grazing, fire, mining operations, game management, water erosion, forest cover, etc. "As to the most desirable kind of forest cover needed to promote the maximum water yield, much yet remains to be learned". Special studies are being made on stream flow in relation to precipitation, on the capacity of soil mantle and surface rock to absorb rainfall and snow-melt and to store moisture. Fellows discusses the view that a watershed should, as far as possible, be maintained in a primeval condition, since in that state it probably provided a good, and well regulated, supply of clear water. The Board's problem, however, is to induce nature to release more water from the catchment area. To achieve this, "nature must be coaxed and not bullied". "If the latter approach is used, nature will surely revolt and the last state will be worse than the first". The underlying argument put forward by Fellows is that, "where high water-yield is the primary objective, it is probable that the concept of the multiple-use of forests has a better chance of adoption than under any other conditions".

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